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FIG. 1.—*Lyginopteris oldhamia*. Restoration. For description see text, p. 55.

5.

STUDIES IN FOSSIL BOTANY

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OF PLANTS,' ETC.

"Nous devons donc envisager l'état présent de l'univers, comme l'effet
de son état antérieur."—*Laplace*.

THIRD EDITION

VOL. II
SPERMOPHYTA

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PREFACE TO THIRD EDITION

VOLUME II

IN the present volume the account of the so-called "Seed Ferns" (Pteridosperms; Chapters I.-III.) has been completely rearranged, and for the most part rewritten.

Since the previous edition appeared, the author's views as to the relationships of the Pteridosperms have changed. The theory that they were derived from Ferns no longer appears tenable. The Seed Plants, of which the Pteridosperms seem to be the most "primitive" representatives known, are now regarded as an independent phylum, running back as far as any of the recognised lines of the Higher Cryptogams.

Chapter I. (Lyginopterideae) now begins with *Heterangium*, which, on anatomical grounds, is taken before the type-genus *Lyginopteris* (the old *Lyginodendron*). The account of the seeds referred to this family has been considerably extended.

Chapter II. is practically new, and illustrated almost entirely by new Figures. The families considered are now dealt with fully, and their mutual relations discussed.

In Chapter III. we return to those Pteridosperms in which there is direct evidence for the mode of reproduction. Various outlying groups are also considered.

In Chapter IV. (Cordaitales) the more advanced families of Palaeozoic Gymnosperms are considered. Prof. Gordon's important discoveries in the early group of the *Pitys* trees are recorded in his own words and illustrated

from photographs which he has supplied. Under the family Cordaiteae several additional genera (notably the new genus *Mesoxylon*) are now included.

In Chapter V. (Mesozoic Gymnosperms) much greater stress is now laid on the Williamsonian Tribe, the older, and, as Dr. Wieland has taught us, the more important line of the great Cycadeoid phylum. A number of new discoveries are recorded, among which Dr. Marie Stopes's extraordinary Cycadeoid fruit from the Gault deserves special mention.

The final chapter (General Results) has again been completely recast. The discovery of the early Devonian land plants, described in Volume I., has profoundly affected the whole aspect of plant-evolution; we have learnt much more, but the effect has been rather to open up new questions than to solve the old.

The following Figures (52 in number) appear for the first time in this edition: Figs. 8, 10, 17, 20, 21, 28, 36, 41-53, 56-67, 75, 76, 84, 94-97, 100, 103, 104, 112, 114, 115, 123, 124, 132-136.

The author is much indebted to the skill of Mr. G. T. Gwilliam, F.R.A.S., in drawing or re-drawing a number of the new illustrations.

Among those to whom special thanks are due for the loan of Figures and other kind help may be mentioned: Dr. Agnes Arber, Prof. Paul Bertrand, Prof. W. T. Gordon, Dr. R. Kidston, F.R.S., Prof. B. Kubart, Prof. F. W. Oliver, F.R.S., Prof. A. C. Seward, F.R.S., Dr. Marie C. Stopes, and Mr. H. Hamshaw Thomas.

Mrs. D. H. Scott, F.L.S., has again undertaken the preparation of the Index.

It may be of interest to some readers to know that the Scott Collection of fossil slides, like the Williamson Collection, is now at the British Museum (Natural History) and open to consultation by students.

D. H. SCOTT.

April 10, 1923.

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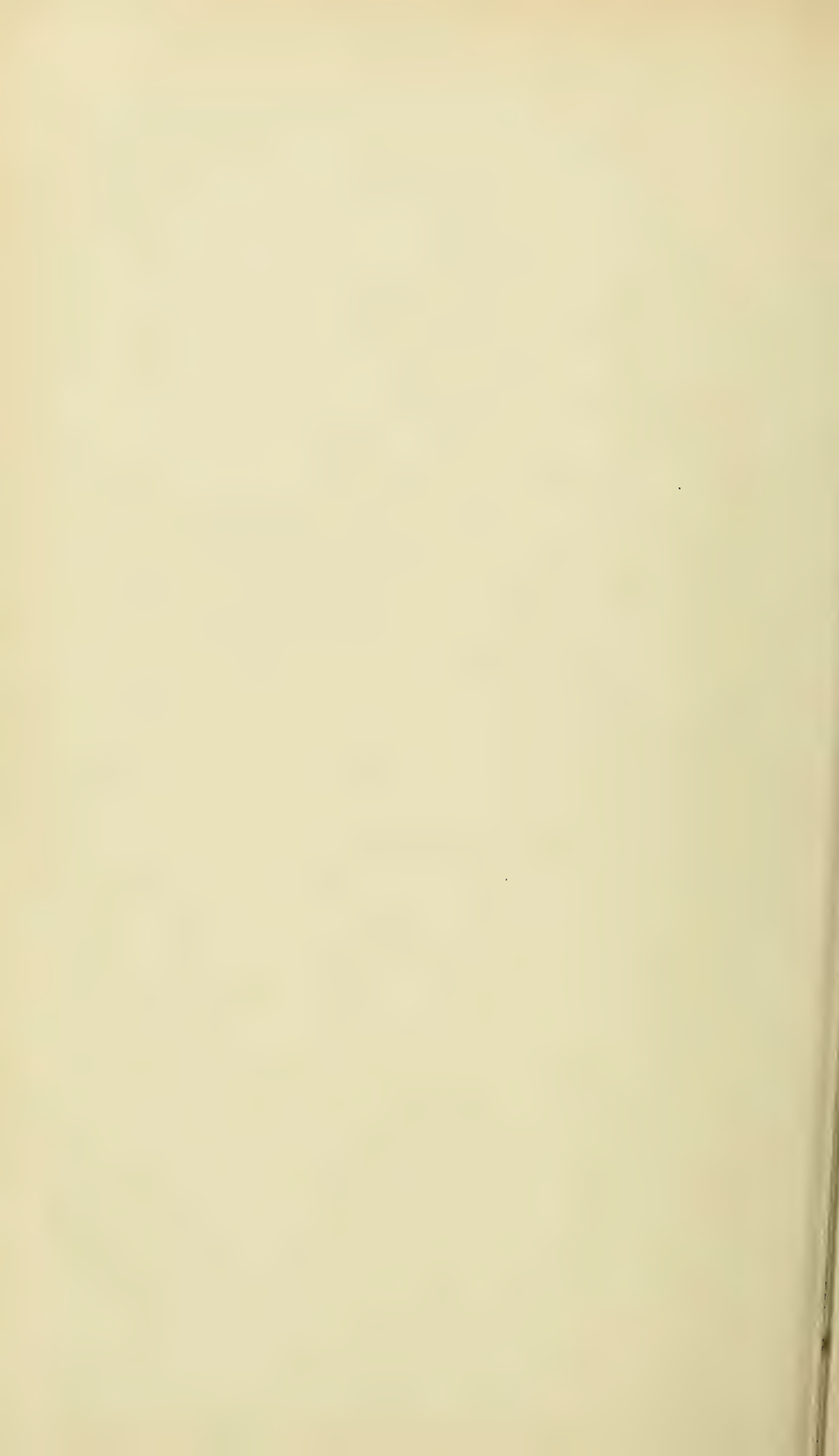
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STUDIES IN FOSSIL BOTANY

VOL. II—SPERMOPHYTA

CHAPTER I

PTERIDOSPERMEAE

Lyginopterideae

WE now leave the Cryptogams, and pass on to the Pteridospermeae, a series of forms which are among the most interesting made known to us by fossil botany, for they appear to unite in their organisation the characters of two of the main divisions of the Vegetable Kingdom—the Seed-plants and the Ferns.

It had been recognised many years ago that some of the fronds from the Carboniferous strata, commonly described as those of Ferns, were subject to grave suspicion of not having really belonged to the class Filicineae. Such suspicions attached not only to the so-called genera *Alethopteris* and *Neuropteris*, and to a large part of *Sphenopteris*, but to an actual majority of the Fern-like fronds. The plants in question had never been found with recognisable fructifications of a Fern-type, whereas in the accepted fossil Ferns, specimens with sori occurred in a fairly large proportion of cases. It was on such negative evidence as this (which is not without its value, if drawn from sufficiently numerous instances) that Stur in 1883 based his exclusion of certain of these genera from Ferns and their reference to Cycads. Subsequently, a large body of well-ascertained positive data accumu-

lated, derived mainly from anatomical investigation, on which, indeed, we then had to depend, for in none of the plants concerned were the organs of reproduction known with certainty up to the year 1903. The anatomical characters observed indicated a position intermediate, at least in certain respects, between Ferns and Gymnosperms, the particular class of Gymnosperms approached being that of the Cycadophyta. Hence the convenient name *Cycadofilices* was applied by Prof. Potonié to the group, and generally adopted.

The remarkable progress made from 1903 onwards left no doubt that most, if not all, the members of this intermediate group, which embraces the majority of the Fern-like plants of the Palaeozoic, bore seeds. They thus proved to be much nearer Gymnosperms than appeared before, but on account of vegetative and other characters they retained an intermediate position, and are now associated under the name Pteridospermeae. This class may be provisionally defined as :

Plants resembling Ferns in habit and occasionally in anatomical characters, bearing seeds of a Cycadean type ; seeds and microsporangia borne on fronds only slightly modified as compared with the vegetative leaves.

The Pteridosperms were thus, as Van Tieghem has said, " Phanerogams without flowers."

We begin with the family Lyginopterideae (formerly Lyginodendreae ; see below, p. 21) ; the genus *Heterangium* is taken first, on account of its age and anatomical characters.

LYGINOPTERIDEAE

HETERANGIUM

The genus *Heterangium* was founded by Corda in 1845,¹ on fragmentary specimens from the coal-balls of

¹ Corda, " Flora Protogaea " — *Beiträge zur Flora der Vorwelt*, Prag, 1845 (2nd ed. Berlin, 1867).

Bohemia, of Middle Coal-measure age. Corda examined the anatomy as well as he was able, and his generic name indicates his view that the wood was composed of two kinds of vessels, large and small. The larger elements were the tracheides of the primary wood, but the smaller were confused with the intermingled cells, which have no claim to the name of vessels. Corda called his species *H. paradoxum*, which is thus the type-species of the genus. But, though better specimens have since come under observation,¹ it is still one of the most imperfectly known species, and our description will, in the first instance, be based on a form described by Williamson in 1873 from the Pettycur deposit,² and named by him, first *Dictyoxyton* and then, on recognising its affinity with Corda's specimens, *Heterangium Grievii*. This is at present the best known of all the species; it is also the oldest, for it is the only one of Lower Carboniferous age of which the structure has been investigated; anatomically, it is one of the simplest forms. This species may therefore best serve as our starting-point.

H. Grievii

The stem of *Heterangium Grievii* was of considerable height and slender form, reaching a diameter of about 2 cm.; as Williamson said, it "always appears in the form of straight, slender, unbranched stems." Its proportions are shown both in the larger petrified fragments and in impressions, such as those named *Sphenopteris elegans*, which there is good reason to believe belonged to this plant (Fig. 2). The outline of the stem is angular, owing to the rapid succession and decurrent attachment of the leaf-stalks (Fig. 4). The leaves, as shown in these impressions (Fig. 3), were of considerable size and highly

¹ Kubart, 1911 (see p. 12).

² Williamson, "On the Organisation of the Fossil Plants of the Coal-measures, Part iv., *Dictyoxyton*, *Lyginodendron* and *Heterangium*," *Phil. Trans. Royal Soc.* 1873, pp. 377-408.

compound, like the fronds of such recent Ferns as some species of *Davallia*.

The Stem.—The anatomy of the stem, though simple,

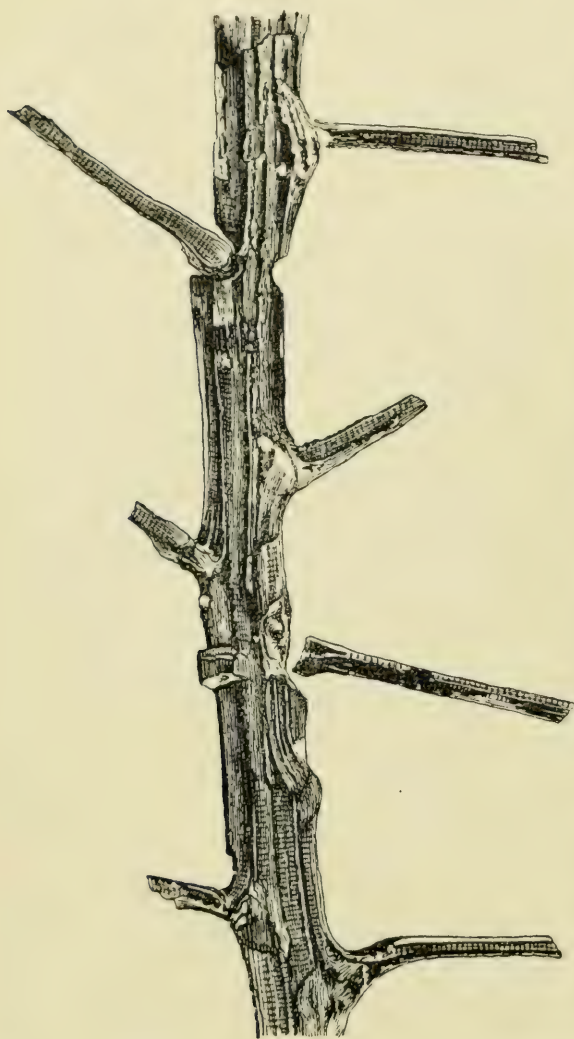


FIG. 2.—*Sphenopteris elegans* (probably = *Heterangium Grievii*). Ribbed stem, bearing several petioles. Note the transverse marks on the surface, where the inner cortex is exposed, corresponding to the sclerotic bands of *H. Grievii*, as shown, for example, in Fig. 4. $\frac{2}{3}$ nat. size. After Stur.

is highly characteristic. There is a single, large vascular cylinder, of the type called a *protostele*, for no pith is present, the wood extending to the centre of the stele. The tracheides are in groups, intermingled throughout with cellular tissue, forming an irregular network (Figs. 4, 5). In all the inner part of the wood the tracheides are of one kind, large elongated elements, with several rows of bordered pits on each wall, whichever way it may face. The cellular tissue between the tracheal groups is thin-walled.

At the outer border of the primary wood, with which alone we are concerned at the moment, the xylem-strands have a more differentiated structure. It is here that the spiral elements, the protoxylem, from which the

development of the wood started, are placed. They lie in the interior of each of the peripheral xylem-strands,

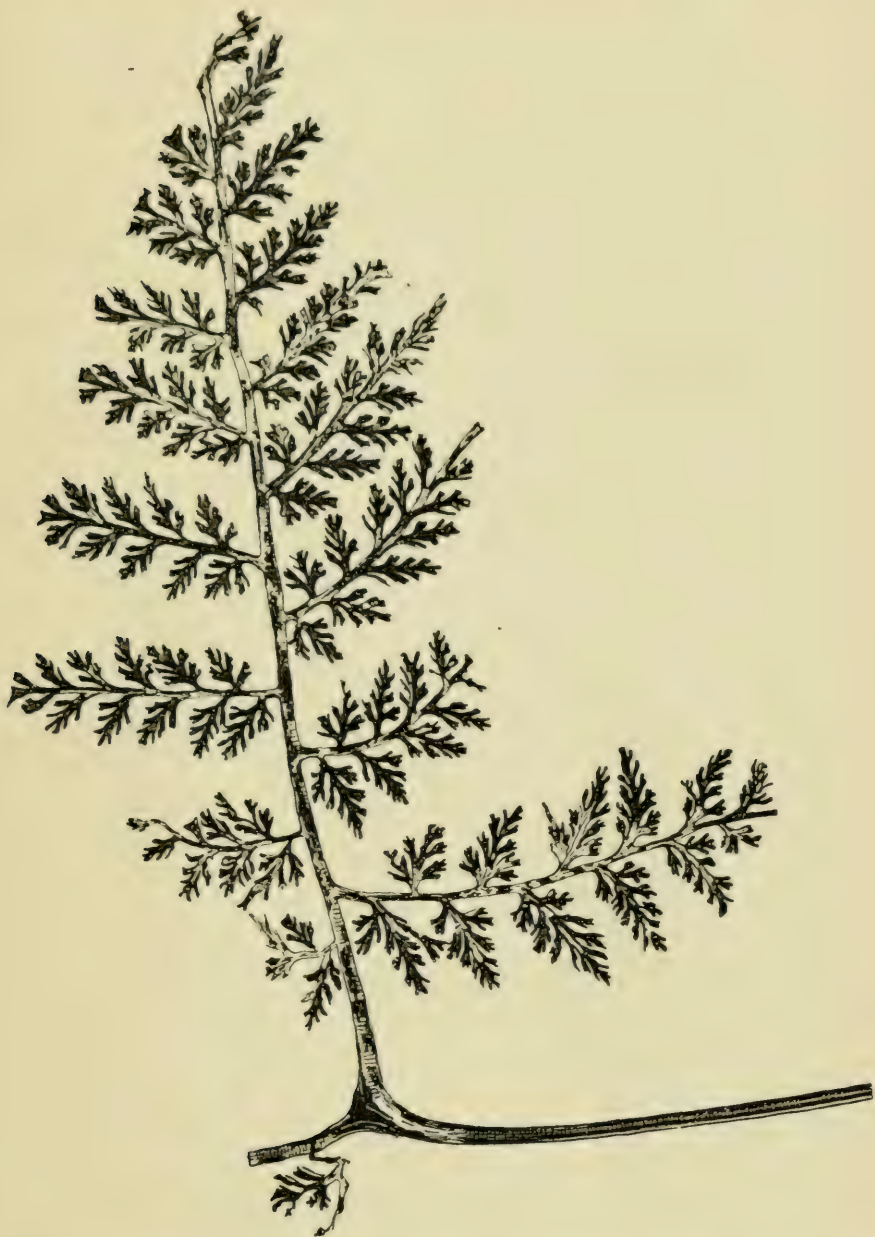


FIG. 3.—*Sphenopteris elegans* (probably foliage of *Heterangium Grievii*). Part of frond. Note the transverse bands on the rachis, as in Fig. 2. $\frac{2}{3}$ nat. size. After Stur.

accompanied by a few thin-walled cells. The strand thus has a *mesarch* structure, the xylem being developed

partly in a centripetal and partly in a centrifugal direction (Fig. 6). The centrifugal portion is relatively small, only a few layers of tracheides lying outside the protoxylem. The centrifugal elements are in immediate contact with the protoxylem, and have a spiral or scalariform sculpture on their walls; the inner or centripetal part of the xylem-strand, separated from the protoxylem

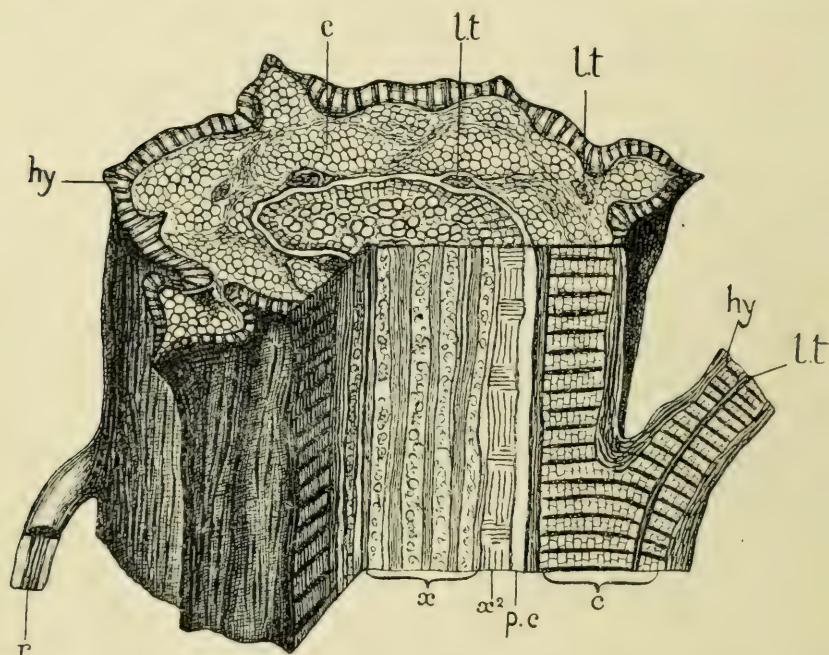


FIG. 4.—*Heterangium Grievii*. Restoration of a portion of the stem, showing transverse and longitudinal section, and part of the external surface. *x*, primary wood of stele; *x*², secondary wood; *p.c*, phloem and pericycle (left blank); *c*, cortex, with horizontal sclerotic bands; *hy*, hypoderma of stem and petioles; *lt.*, leaf-traces, one of which is entering a petiole; *r*, adventitious root. The bases of several petioles are shown. Enlarged. After Williamson, *Phil. Trans.*

by the little island of cellular tissue, is composed, like the rest of the wood, of pitted tracheides (Fig. 7). Hence we may infer that the small, centrifugal portion was the first to be formed after the protoxylem. The peripheral xylem-strands, while easily recognisable from their structure and position, are not sharply delimited from the rest of the primary wood (Figs. 5, 6). A certain number of them form the direct downward prolongation of the leaf-traces, while others appear to be of the nature

of "reparatory strands," which take the place of the leaf-traces as they pass out.

The whole mass of primary wood is surrounded by a zone of phloem, usually ill-preserved, and by a well-marked pericycle of rather large cells.

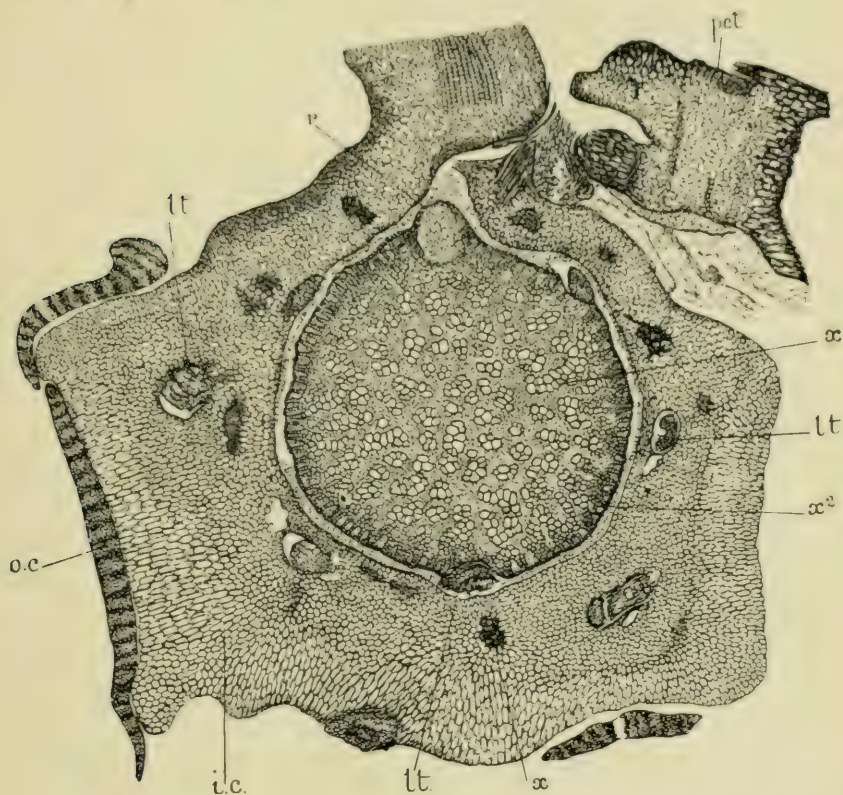


FIG. 5.—*Heterangium Grievii*. Transverse section of stem. x , central mass of primary wood, consisting of tracheides and parenchyma; x^2 , secondary wood, beginning to form; next come phloem and pericycle; $i.c.$, inner cortex (x in this zone is a sclerotic group); $lt.$, leaf-traces; r , base of an adventitious root; $o.c.$, outer cortex or hypodermis (only present in places); pet , base of petiole, partly detached. \times about 5. S. Coll. 396. (G. T. G.)

So much for the primary structure of the stele; in most specimens secondary growth in thickness had taken place. The primary xylem is then surrounded by a zone of radially arranged, secondary wood, not, as a rule, attaining any very great breadth (Fig. 6). The secondary tracheides are generally small compared with those of the primary wood; the bordered pits are for

the most part restricted by the radial walls; medullary rays, often several cells in width, traverse the wood; in this species there is no definite distinction between principal and secondary rays, though some of them are continuous with the network of cellular tissue in the primary wood. The cambium is sometimes preserved; it lies on the outer border of the wood which it had formed, and produced secondary phloem towards the exterior. The process of secondary growth was, in fact, altogether a normal one, anticipating the scheme familiar to us in the higher plants. It is interesting to find this typical mode of growth in thickness already established in a plant, which, in its primary structure, is on a level with one of the lower Ferns.¹

The cortex presents some characteristic features. The inner cortex contains, embedded in the cellular tissue, numerous horizontal plates of thick-walled cells, which may be called stone-cells; the plates succeed one another in regular vertical series (Fig. 4). Within each plate, the cells have a regular arrangement in short vertical rows, indicating that the plate was formed by a special meristem. These horizontal stiffening plates are conspicuous even to the naked eye, and enable us to recognise the plant at a glance when seen in longitudinal section or on the surface of a fracture (cf. Fig. 2).

The outer cortex consists of alternating radial bands of thick-walled fibres and cellular tissue, the former serving to give mechanical strength to the stem, while the latter were in communication with the stomata of the epidermis. The fibrous bands run parallel and are not usually united into a network (Figs. 4, 5).

The Leaf-trace and Leaf.—We have now to consider

¹ There is a fairly close analogy in the structure of the stele between a *Heterangium* such as *H. Grievii* and one of the simpler species of *Gleichenia*. In both, the vascular cylinder is a protostele, the wood consisting of intermixed tracheides and parenchyma, and in both the structure is mesarch, the protoxylem-groups lying some little distance within the periphery of the wood.

the leaf-trace and its connection with the leaf. In this species the leaf-trace is always a single bundle throughout its course, only dividing in the rachis to supply the successive subdivisions of the compound frond. Where it first leaves the stele (cf. Fig. 6), the leaf-trace usually has a single protoxylem-group, which soon splits into two as the strand moves outwards. The trace passes

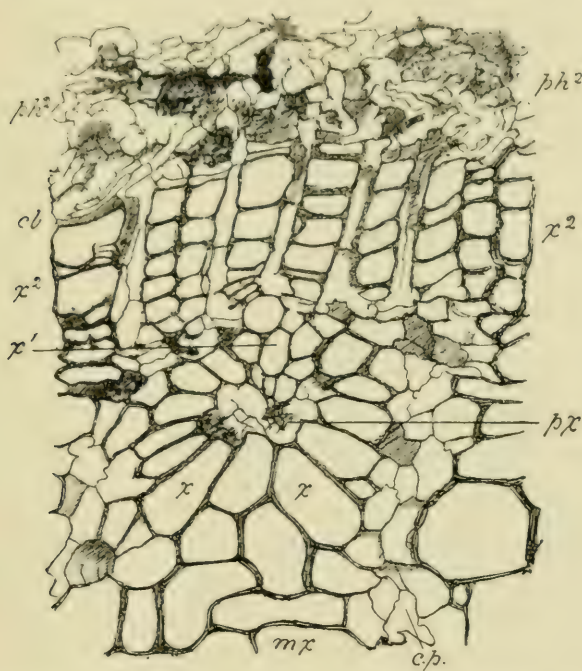


FIG. 6.—*Heterangium Grievii*. Part of transverse section, from outer part of stele, showing a primary xylem-strand and adjacent tissues. *px*, protoxylem of strand; *x*, centripetal, *x*¹, centrifugal, primary wood; *mx*, metaxylem, *c.p.*, conjunctive parenchyma; *x*², secondary wood; *cb*, cambium; *ph*², phloem. $\times 135$. *Phil. Trans.*, W. and S. Will. Coll. 1293.

through the phloem and pericycle, and then very gradually traverses the cortex, so that the traces of a number of the leaves are seen in the same transverse section (Fig. 5). The structure of the trace-bundle is at first collateral, *i.e.* with the phloem on the outer side only, but by the time it enters the leaf-stalk it becomes concentric, the phloem here extending all round the xylem, as in the main foliar bundles of most Ferns. Though the bundle never divides, it becomes somewhat bilobed

in the outer part of its course, and the two halves of the xylem are sometimes separated by a narrow radial band of cells; this fact is of some interest, as faintly foreshadowing the divided leaf-trace characteristic of other species.

The leaves are arranged in a spiral order, the phyllotaxis being $\frac{3}{8}$ in the larger and $\frac{2}{5}$ in some of the smaller stems. The petioles are rather small compared with the stem which bore them; thus in a stem about 2 cm. in diameter the width of the leaf-base is only about 4 mm.

The structure of the foliar bundle remains essentially the same as when it left the stem; it is concentric and mesarch. The cortex of the petiole and rachis contains the same horizontal plates of stone-cells as that of the stem, a fact which has aided in the identification of the foliage when preserved in the form of impressions (Fig. 3). The fibrous bands of the outer cortex are also similar in both organs.

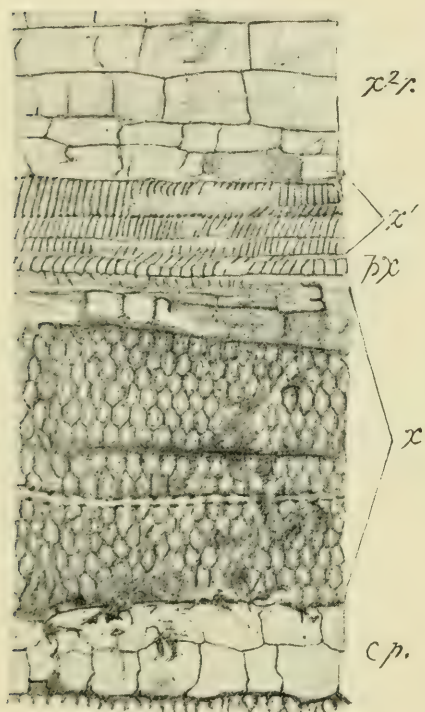


FIG. 7.—Corresponding longitudinal section, showing the structure of the tracheides. x^2r , parenchyma at the commencement of a medullary ray. Other lettering as in Fig. 6. $\times 135$. *Phil. Trans.*, W. and S. Will. Coll. 1266.

The highly compound frond, now identified as belonging to *Heterangium Grievii*, was long previously known under the name *Sphenopteris elegans*, Brongn. (Fig. 3).¹

¹ This identification was originally due to Dr. Kidston, "Fructification and Internal Structure of Carboniferous Ferns," *Trans. Geol. Soc. Glasgow*, 1889, p. 49. When first discovered by Volkmann in 1720 the present *Sphenopteris elegans* was named *Fumaria officinalis*, which is thus a synonym for *Heterangium Grievii*—a strange freak of nomenclature!

This was referred by Stur to his genus *Diplotmema*, characterised by the forking of the rachis of the primary pinnae. Sections of the rachis of *H. Grievii* are sometimes met with in which the vascular bundle has divided into two equal strands; this may represent the bifurcation of the pinna, as described by Stur. It is, however, possible that the main rachis may have also forked, as was the case in the allied genus *Lyginopteris*. The structure of the ultimate leaflets, borne on the rachis, is not known in detail, owing to defects of preservation.

The Root.—The roots of *Heterangium Grievii* were first identified by Dr. Margaret Benson, F.L.S., who found them in connection with the stem, on which they were borne in vertical rows. The larger roots, attaining a diameter of about 4 mm., are almost invariably triarch, that is to say, the central, primary wood has three groups of spiral elements, protoxylem, from which the development started. The smaller roots and rootlets are often diarch. Secondary growth took place in the manner typical of recent roots, *i.e.* the arcs of secondary wood were first formed in the spaces between the protoxylem groups. Opposite each protoxylem there is thus a broad ray, which, however, becomes broken up by the intercalation of a few radial rows of tracheides, usually smaller than those of the woody wedges. The cortex consists of loosely packed cells, and is bounded on the outside by a rather small-celled epidermis.

It will be noticed that these roots are in all respects comparable to those of a recent plant of Gymnospermous affinities. The comparison might equally well be extended to Dicotyledons, if it were not for the absence of vessels, as distinguished from tracheides. True vessels, arising by cell-fusion, have not yet been demonstrated in the wood of any Palaeozoic plant.

Other Species of Heterangium

Heterangium Grievii represents the simplest type of the genus, characterised especially by the leaf-trace consisting of a single vascular strand, while the central cylinder is of a strictly protostelic type, the peripheral strands not being sharply marked off from the rest of the primary wood. The name *Eu-heterangium* has been given to a sub-genus, of which *H. Grievii* is the type. One or two other species of this sub-genus merit a brief mention.

Several species of *Heterangium*, from the Ostrau beds of Upper Silesia, have recently been described by Dr. Kubart.¹ The horizon is Upper Carboniferous, but older than that of our Lower Coal-measures, corresponding to the upper part of the Millstone Grit. Several of these species are referable to the sub-genus *Eu-heterangium*. The simplest is *H. Sturii*, Kubart, a form in which the peripheral strands of the primary wood are even less differentiated than in *H. Grievii*, only becoming distinct when they are given off as leaf-traces. Their structure is nearly exarch, the primary centrifugal xylem being much reduced. This, however, is a character subject to much variation throughout the genus. The leaf-traces appear to be quite undivided. In *H. alatum*, Kubart, the leaf-traces are somewhat more clearly delimited at the border of the stele, and they are again typically mesarch, as in *H. Grievii*. The number of leaf-traces is considerable, as many as ten appearing in the transverse section; they remain undivided. The stem bore crowded leaves, the small winged petioles surrounding the axis. *H. polystichum* is a nearly allied species, in which the

¹ B. Kubart, "Pflanzenversteinerungen enthaltende Knollen," etc., *Sitzungsber. d. K. Akad. d. Wiss. in Wien*, Math.-Naturwiss. Klasse, Bd. cxvii. 1908. "Corda's Sphaerosiderite," etc., *ibid.* Bd. cxx. 1911. "Über die Cycadofilicineen *Heterangium* und *Lyginodendron*," etc., *Österreichische bot. Zeitschrift*, Jahrgang 1914.

leaf-traces are still more numerous, the number in the transverse section being thirteen, probably indicating a $\frac{5}{13}$ phyllotaxis.

H. Schusteri has a stele only a little more differentiated than in *H. Sturii*, but there is the interesting difference that the leaf-traces, which are few and large, divide into

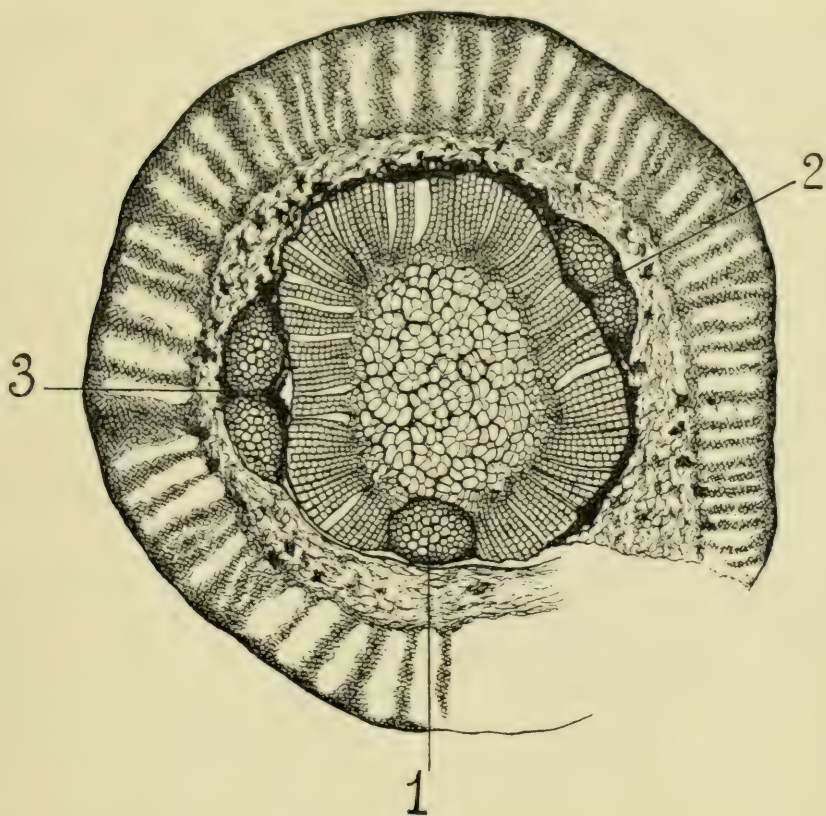


FIG. 8.—*Heterangium Schusteri*. Transverse section of stem, showing primary and secondary wood and cortex, with three leaf-traces (1—3), the two outer dividing. \times about 8. After a photograph by Dr. Kubart. (G. T. G.)

two after leaving the stele (Fig. 8). There is a British species, *H. minimum* (Scott, 1917), which agrees with *H. Schusteri* in this respect. It is convenient to include in the sub-genus *Eu-heterangium*, forms in which the trace leaves the wood as a single strand, even though it may divide once on its outward course.

From the simple type of *Eu-heterangium* other members

of the genus diverge in two directions. On the one hand we have a series of species in which the leaf-trace, from its first starting-point, is *double*, consisting of two separate strands, which further subdivide in the cortex or base of the leaf. At the same time the peripheral strands of the primary wood are somewhat sharply differentiated. Such forms have been grouped in the sub-genus *Polyangium*.¹

On the other hand there are certain species in which the central part of the stele has undergone a change: a pith has begun to develop, the cellular tissue of the primary wood increasing at the expense of the tracheal groups. These forms constitute a clear transition to the next genus, *Lyginopteris*, and it is proposed to include them under a third sub-genus, *Lyginangium*. We will take the sub-genus *Polyangium* first.

Three closely allied species are known from the British Lower Coal-measures, and others, from the Upper Coal-measures of France, seem to belong here also.² The most interesting species is *H. tiliaeoides*, described by Williamson in 1887, for the specimens are in many respects exceptionally well preserved.³ The structure of the primary wood is somewhat more regular than in *H. Grievii*, consisting of a number of fairly definite groups or packets of tracheides, separated by a network of cellular tissue. The peripheral xylem-groups are somewhat sharply delimited, and where secondary wood had developed, it is traversed by large, principal rays, corresponding to and in connection with the cellular tracts separating the primary peripheral strands. The

¹ D. H. Scott, "The Heterangiums of the British Coal-measures," *Linnean Society's Journal, Botany*, vol. xlv. 1917.

² Renault, "Bassin houiller et permien d'Autun et d'Épinac," *Flore fossile*, ii. pp. 248-260, 1896, and the earlier papers there cited.

³ Williamson, Part xiii., "*Heterangium tiliaeoides*," etc., *Phil. Trans. Royal Soc.* 1887, B; Williamson and Scott, "Further Observations, etc., Part iii., *Lyginodendron* and *Heterangium*," *ibid.* vol. 186, B (1895).

centrifugal portion of the primary xylem in these strands is little developed, the structure approaching the exarch condition more nearly than in *H. Grievii*.

To form the trace of each leaf, two perfectly distinct strands depart from the stele. Thus the leaf-trace, from its first origin, is double. The two

strands subdivide in passing through the cortex, and there are thus four separate bundles in the petiole. The pericycle is very wide and often contains groups of stone-cells, like those in the cortical plates. But the most remarkable feature of the species is the great development of the phloem, which in several cases equals the secondary wood in thickness.

The rays, where they pass through the phloem-zone, are dilated outwards, like those of the Lime tree, a fact to which the

species owes its name. The sieve-tubes are often wonderfully preserved, the numerous sieve-plates on the radial walls appearing as clearly as in the tissues of a recent plant (Fig. 9). This is a rare though not unprecedented case among fossil plants. The sieve-tubes have very much the same structure as in recent Cycads. The cortex is similar to that of the species already considered.

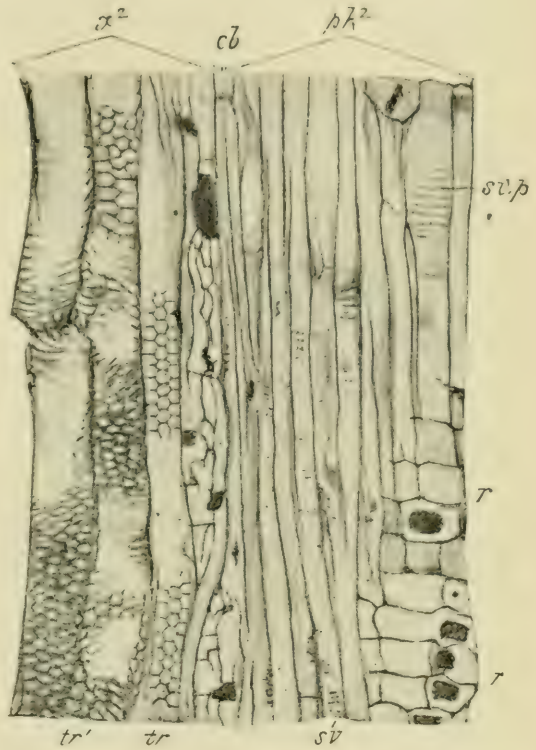


FIG. 9.—*Heterangium tiliacoides*. Radial section through part of secondary wood and phloem. x^2 , secondary wood; tr' , fully developed pitted tracheides; tr , tracheides with pits beginning to form; cb , cambium; ph^2 , secondary phloem; sv , sieve-tubes; $sv.p.$, sieve-plate; r , phloem-ray. $\times 112$. *Phil. Trans.*, W. and S. Will. Coll. 1628.

The adventitious roots of *H. tiliacoides* are known ; they do not differ essentially from those of *H. Grievii*, but appear to be usually tetrarch or pentarch, whereas in that species triarch structure prevails.

The great feature in which *H. tiliacoides* differs from *Eu-heterangium* is the compound leaf-trace, the character of the sub-genus *Polyangium*. This is even more

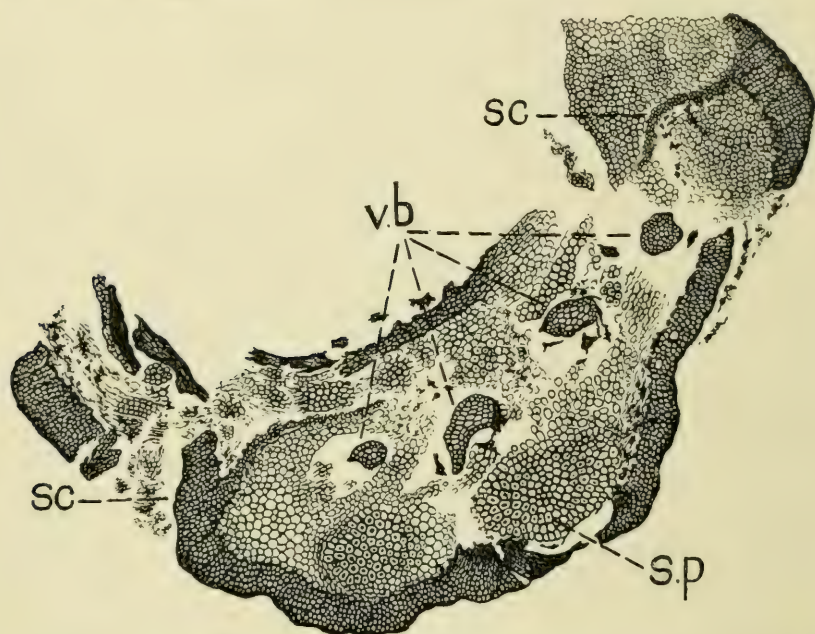


FIG. 10.—*Heterangium shoreense*. Transverse section of leaf-base, attached to cortex of stem *v.b.*, the four vascular bundles ; *sc*, sclerenchyma delimiting the leaf-base on either side ; *s.p.*, sclerotic plate. $\times 6$. S. Coll. 2787. (G. T. G.)

strikingly shown in another species, *H. shoreense*.¹ Here, as in *H. tiliacoides*, the trace is double on first leaving the stele ; in passing through the cortex each strand divides into two, so that the leaf-base contains four bundles (Fig. 10) ; a further subdivision then takes place, the petiole containing as many as eight bundles—a wide departure from the simple structure of *H. Grievii*.

The third British representative of the sub-genus

¹ This is from Shore, Littleborough, Lancs, while *H. tiliacoides* is a Yorkshire species, from the Halifax Hard Bed.

Polyangium, *H. Lomaxii*,¹ agrees in the behaviour of the leaf-trace with *H. tiliacoides*, but is remarkable for the frequent wide separation of the two bundles of the trace, owing to the presence of a vertical series of adventitious roots between them. This species, of which several forms are known, is also interesting from the fact that the stem, in one instance, has been observed to branch, the only case in which branching of the stem has so far been recorded in the genus *Heterangium*. The branch is of small size compared with the parent stem, but agrees with it essentially in structure.² The stone-cells of the inner cortex are remarkably well developed in some specimens of *H. Lomaxii*; they form massive groups, many cells thick, differing from the comparatively thin sclerotic plates of *H. Grievii*.

All the three species just described are characterised, apart from the compound leaf-trace and polydesmic petiole, by the well-marked delimitation of the peripheral xylem-strands, and by the tendency to exarch structure in the vascular bundles. The former character indicates a slight departure from the pure protostelic type, owing to a progressive downward differentiation of the leaf-trace system. The exarch condition is never completely attained, for a little primary centrifugal wood always persists, so far as hitherto observed.

Four species described by Renault from the Upper Coal-measures of Autun appear to be referable to the sub-genus *Polyangium*. Three of them, *H. punctatum*, Ren., *H. Renaultii*, Brong., and *H. Duchartrei*, Ren., are so similar that they may perhaps all be forms of one species. They have a general resemblance to the British *H. tiliacoides*. Renault's fourth species, *H. bibractense*, is remarkable for the small size of the primary, and the great development of the secondary wood; while the

¹ From Dulesgate, Lancs. All the known specimens came from a single coal-ball.

² Williamson and Scott, *l.c.* 1895.

former is only from 1 to 1.5 mm. in diameter, the latter attains a thickness of nearly a centimetre.

It will be noticed that the *Polyangium* species are generally of later geological age than those of the simpler, *Eu-heterangium*, type. Of the latter, one, *H. Grievii*, is Lower Carboniferous, the four Ostrau species are from a low horizon (Millstone Grit) of the Upper Carboniferous, while only one species (*H. minimum*) is as late as our Lower Coal-measures. On the other hand, the species referred to *Polyangium* are all of Lower or Upper Coal-measure age.

The sub-genus is interesting as showing a marked advance on the simple organisation which was once supposed to be characteristic of *Heterangium*. *Polyangium*, however, does not appear to lead to anything higher than itself. It presents interesting analogies, as regards leaf-trace and petiole, with groups, such as Calamopityeae and Medulloseae, to be later described, but there is no evidence of any direct evolutionary connection.

It is very different with the third group of species, to which it is proposed to assign the sub-generic name *Lyginangium*, for they appear to lead directly to the next genus, *Lyginopteris*. To anticipate a little here, we may point out that *Lyginopteris*, in its typical form (e.g. in a full-sized stem of *L. oldhamia*), is characterised by possessing a large pith, the central part of the primary wood having wholly disappeared, being replaced by cellular tissue, leaving only the peripheral strands to represent the original protosteles. At the same time the peripheral xylem-strands are themselves reduced in number, those only persisting which are either themselves leaf-traces or are in immediate connection with them.

The forms connecting *Heterangium* with *Lyginopteris* were all discovered by Dr. Kubart.¹ *Heterangium Andrei* is one of the Ostrau species. The stem may

¹ Kubart, *l.c.* 1914.

still be called protostelic, for the xylem extends to the centre, but the more central tracheides are scattered, the cellular tissue beginning to predominate. The peripheral xylem-strands are very distinct and few in number. If we compare a section of *H. Andrei* with that of a typical *Lyginopteris*, such as *L. oldhamia*, the general similarity at once strikes the eye; the resemblance even extends to the presence of peculiar stalked glands on stem and petiole. In *H. Andrei* a single leaf-trace starts from the stele, divides into two on its outward course, and subdivides into four on entering the leaf-stalk.

In this species we have a combination of the characters of *Heterangium* and *Lyginopteris*, though the former are still predominant. In another species, *H. intermedium*, from a different locality (Westphalia) and a somewhat higher horizon (Middle Coal-measures), Dr. Kubart finds an even nearer approach to *Lyginopteris*, but details are still unpublished.

To complete the story of the transition, we must pass on at once to the next genus, for there is no real break in the series.¹

LYGINOPTERIS

Lyginopteris heterangioides, Kubart, another of the Ostrau species, is, in all respects save one, a typical *Lyginopteris*. There is an extensive pith around which the few xylem-strands, only six in number, and all forming part of the leaf-trace system, are ranged. But in the middle of the pith a few tracheides are constantly present, an evident vestige of the central primary wood of *Heterangium*, already becoming more and more reduced in *H. Andrei* and *H. intermedium*. As Dr. Kubart, the discoverer of the transitional forms, says: "We have before us a continuous series, in which the protostele

¹ For the sake of continuity the vegetative structure is treated consecutively. The reproductive organs of the family are described later (p. 63).

slowly becomes a siphonostele." The latter, a tubular stele with a pith, is the form of vascular cylinder characteristic of the higher plants.

We may also look at the transition from a somewhat different point of view. The protostele, with its solid axis of primary wood, is clearly a primitive form of vascular organisation. It is found among the simpler and more ancient Ferns and Lycopods, throughout the extinct Palaeozoic group of the Sphenophylls and in the oldest known phylum, the Devonian Psilophytales. Where this type of structure prevails, the leaf-traces (where they exist) play a subordinate part—they are in connection with the stele, but do not build it up. Now, in the higher plants, both Gymnosperms and Angiosperms, the whole vascular system of the stem has come to be a leaf-trace system; all the vascular strands of the stele can be accounted for as the downward prolongations, variously fusing, of the bundles which pass in from the leaves.

In *Eu-heterangium* we have the more primitive condition; the leaf-traces contribute only a subordinate part to the stele, and when they have once entered it, soon lose their individuality. In the sub-genus *Polyangium*, they show a little more independence, but the central wood persists, and is still predominant. In the sub-genus *Lyginangium*, while the peripheral strands increase in distinctness and show a more direct relation to the leaves, the central xylem begins to dwindle. In *Lyginopteris heterangioides* it is reduced to a mere vestige, and the primary wood is represented almost wholly by the leaf-trace system. In the rest of the genus the central xylem has disappeared altogether. It is entirely replaced by pith, and only the leaf-traces remain; *i.e.* that part of the vascular system which is in direct communication with the leaves alone persists. That the rest of the primary xylem can be dispensed with, is explained by the increasing development of the secondary wood, which replaces, in

a more adaptable form, the non-leaf-trace xylem of the protostele.

Having briefly traced the transition from *Heterangium* to *Lyginopteris*, it will now be most profitable to study the structure of the latter genus in its type-species, *Lyginopteris oldhamia*, Binney, in which the anatomy of all the organs is known.

L. oldhamia

Lyginopteris oldhamia is a plant of the Lower and Middle Coal-measures, extremely common in the coal-balls of Lancashire and Yorkshire, and also occurring in those of Westphalia at a somewhat higher horizon. It is quite possible, and even probable, that under the specific name more than one species is embraced, the name thus representing a type of structure rather than a single plant, but the forms included under it have not yet been specifically discriminated. On the other hand, the species described by Dr. Kubart from the Ostrau beds seem to be quite distinct from ours.

Lyginopteris oldhamia was discovered and briefly described by Binney in 1866 under the name *Dadoxylon oldhamium*.¹ Our full knowledge of its structure is due to Williamson, who described the stem in 1873, first calling it *Dictyoxylon oldhamium* and then placing it in Gourlie's genus *Lyginodendron*, based on cortical impressions, with which Williamson identified his structural specimens. It has turned out, however, that Gourlie's type-specimens belonged to quite a different group of plants (Lepidodendreae); his name *Lyginodendron* is still used in its original sense for reticulate cortical impressions, which, as a rule, have nothing to do with the plant described

¹ E. W. Binney, *Proc. Lit. and Phil. Soc. Manchester*, 1866; E. A. N. Arber, "Notes on the Binney Collection of Coal-measure Plants, iii. The type-specimens of *Lyginodendron oldhamium* (Binney)," *Proc. Cambridge Phil. Soc.* vol. xi. 1902.

by Binney and Williamson. Hence the name *Lyginodendron* for the latter type has been abandoned, and we now use the generic name *Lyginopteris*, proposed by Potonié in 1899.¹

All the vegetative parts of *Lyginopteris oldhamia* are known, not to mention the reproductive organs, which will be dealt with later. The history of our knowledge of the species may be said to go back to 1829, when Brongniart described and figured the external characters of the foliage in *Sphenopteris Hoeninghausi*, which there are strong grounds for identifying with the petrified specimens of *L. oldhamia*, discovered nearly forty years later. The restoration in the frontispiece will serve to give an idea of the general habit of the plant.

The Stem.—The dimensions of the stem are very variable, the largest specimens having a diameter of about 4 cm. and the smallest of about 2 mm. The stem is known to have frequently branched, at least in some forms of the plant. Our description will, in the first instance, be based on the larger stems, which best show the structure which we may regard as typical.

In all specimens of *L. oldhamia*, as in other species of the genus, there is a well-developed pith, usually of large size relatively to the stem as a whole (Fig. 11). Around the pith a number (5—10) of scattered xylem-strands, belonging to the leaf-trace system, are disposed in a ring. Outside this, in all but the youngest specimens, we find a zone of secondary wood; then follows the phloem, secondary and primary. Beyond the phloem is a well-marked pericycle, usually with a zone of periderm; this completes the stele. We next reach the inner cortex, of parenchymatous structure, and then the very characteristic outer cortex, consisting of a network of radial fibrous bands, with cellular tissue in the meshes. In favourable cases a few external layers of cortex, with

¹ Potonié, *Lehrbuch der Pflanzenpaläontologie*, p. 170, Berlin, 1899; Seward, *Fossil Plants*, vol. iii. pp. 36-38, Cambridge, 1917.

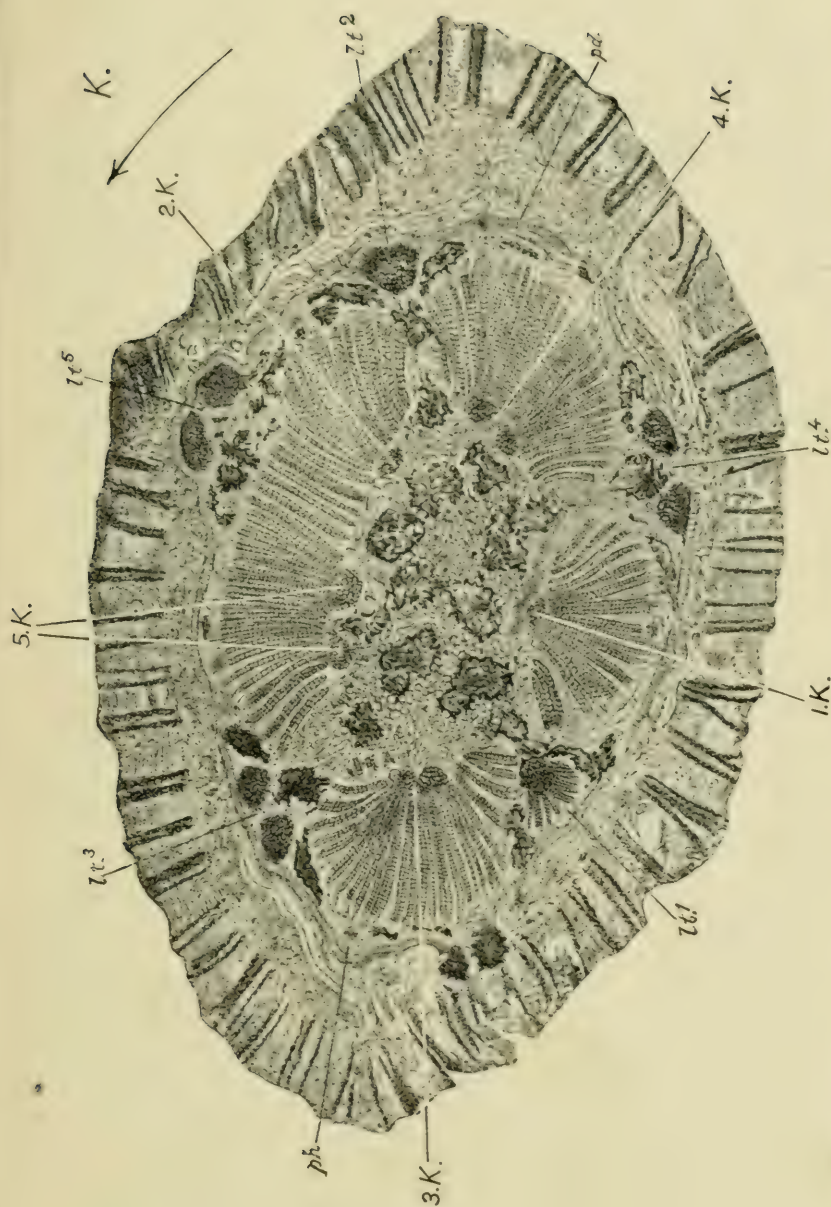


FIG. 11.—*Lyginopteris oldhamia*. Transverse section of stem. Surrounding the pith, which contains nests of sclerotic cells, are eight primary xylem-strands; beyond these is the wide zone of secondary wood, and then the phloem. *ph*, a primary phloem-group; *pd*, periderm, marking the outer limit of the pericycle. Beyond the periderm is the inner cortex, and at the exterior, the outer cortex, with the dark radial bands of sclerenchyma. *lt.1*—*lt.5*, the five leaf-traces, numbered in the order of the phyllotaxis, *lt.3* belonging to the lowest leaf of the series. The arrow *K* marks the cathodic direction. *1.K.*—*5.K.*, the cathodic strands, single or already divided, from which the succeeding leaf-traces will be supplied. See diagram, Fig. 17. $\times 4\frac{1}{2}$. *Phil. Trans.*, W. and S. S. Coll. 270.

the epidermis, may be preserved. The bases of the leaves are frequently found in connection with the stem; the usual phyllotaxis was $\frac{2}{5}$. In all the tissues of the stem, from the wood outwards, leaf-traces are met with on their way out to the leaves.

We will now consider the various tissues more in detail. The pith consists of a matrix of large, short cells, among which very characteristic groups of dark, thick-walled elements are embedded (Fig. 11); these are known as the "sclerotic nests." The cell-walls are sometimes extremely thickened and stratified. The cells of each nest are usually ranged in vertical rows, and the whole body is comparable to one of the plates of stone-cells in *Heterangium*, though the distribution of the groups is different.

Passing on to the vascular tissues, we find that the primary wood of the stele consists solely of the isolated xylem-strands surrounding the pith. Each strand has mesarch structure, and closely resembles a peripheral xylem-strand of *Heterangium Grievii* (Fig. 6). The protoxylem lies nearer the outer than the inner edge of the strand, but is so placed that there is quite an appreciable amount of primary centrifugal xylem (Fig. 13). Here, as in *Heterangium*, an island of cellular tissue adjoins the protoxylem, which is in contact with the centrifugal part of the strand; the elements of this part are spiral or scalariform, while those of the centripetal xylem are pitted (cf. Fig. 7). The pitting is multiseriate, as in *Heterangium*, and in the case of the primary tracheides is present on all the walls alike.

We see, then, that not only has the whole of the central wood of *Heterangium* disappeared, having been replaced by pith, but that only a few of the peripheral xylem-strands remain, namely, those which are in the most direct connection with the leaves. But those strands which still persist are identical with the corresponding parts of the primary wood of *Heterangium*. Williamson

recognised from the first the close affinity of the two genera, and this has been confirmed by all subsequent research.

When secondary growth begins, the spaces between the primary xylem-strands are at once bridged over by the activity of the interfascicular cambium, so that the secondary wood forms a practically continuous zone, interrupted only by the outgoing leaf-traces (Figs. 11, 12).



FIG. 12.—*Lyginopteris oldhamia*. Transverse section of stem (structure as in Fig. 11), surrounded by a mass of foliage, showing rachis and leaflets cut in various directions. On the left, the stem is giving off an adventitious root. $\times 4$. From a photograph by Mr. L. A. Boodle. S. Coll. 636.

It has, however, a lax structure, due to the presence of numerous, and often wide, medullary rays. As growth goes on, new rays are added between the old. The structure of the secondary wood is the same as in *Heterangium*; the multiseriate bordered pits, of which there may be as many as seven rows on the wall, are, as a rule, limited to the radial faces of the tracheides. Where the preservation is good, it can be seen that the pore of the pit has the form of an inclined slit. The rays, as is usually the case, consist of muriform cellular tissue.

The cambium itself is often well preserved (Fig. 16). Where a ray is being formed, the tangential divisions are few, and the cambial cells are therefore longer in the radial direction than elsewhere.

In good sections a group of primary phloem can be clearly recognised opposite each of the primary xylem-strands (Fig. 16). The cambium adds a considerable thickness of secondary phloem, distinguished by the

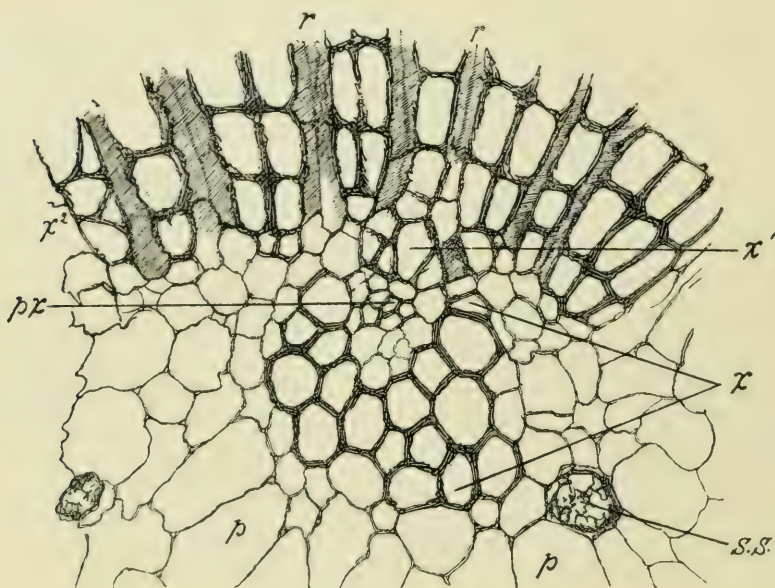


FIG. 13.—*Lyginopteris oldhamia*. Part of transverse section of stem, showing a primary xylem-strand, and adjacent tissues. *px*, protoxylem; *x*, centripetal primary wood; *x¹*, centrifugal primary wood; *x²*, secondary wood; *r*, medullary rays; *p*, pith; *s.s.*, secretory sac. $\times 100$. *Phil. Trans.*, W. and S. Will. Coll. 1884.

radial seriation of its elements. It is broken up into narrow groups by the numerous phloem-rays, and consists of larger and smaller elements, in tangential layers; the former appear to have been the sieve-tubes.

The pericycle, outside the phloem, is a well-marked zone of short cells, among which many sclerotic nests, like those of the pith, are embedded. In the outer layers of the pericycle, a phellogen arises, which forms, on its outer side, a conspicuous internal periderm (Figs. 14, 16). We have not, however, observed any case in

which the cortex outside the periderm had been ex-

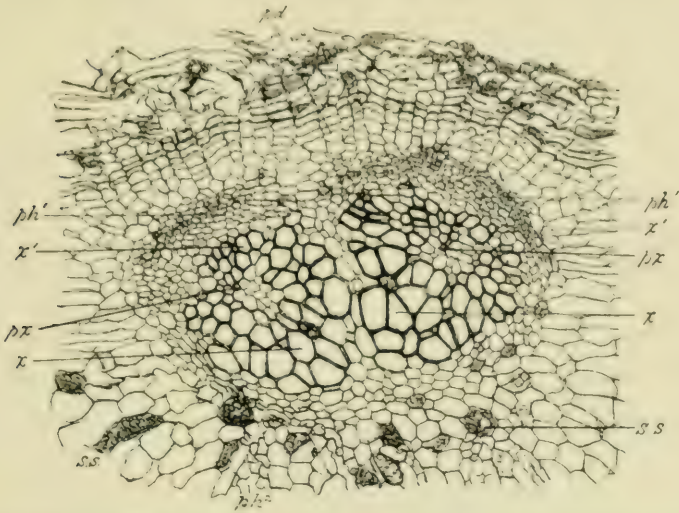


FIG. 14.—*Lyginopteris oldhamia*. Part of transverse section of stem, showing a double leaf-trace, and adjacent tissues. *px*, protoxylem of bundles; *x*, centripetal, *x'*, centrifugal, part of xylem; *ph'*, phloem of leaf-trace; *ph²*, phloem of stele; *s.s.*, secretory sacs; *pd*, periderm. \times about 40. *Phil. Trans.*, W. and S. Will. Coll. 1884.

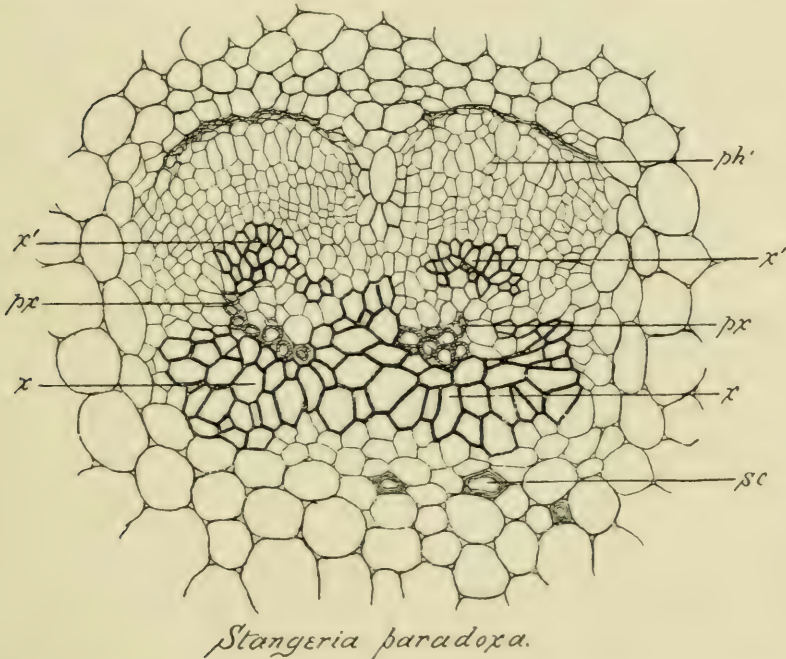


FIG. 15.—*Stangeria paradoxa*. Part of transverse section of petiole, showing a double bundle to compare with Fig. 14. *sc*, stone-cell. Other lettering as in Fig. 14. \times 95. From a drawing by Mr. G. Brebner.

foliated, though the imperfect preservation of the inner

cortex may perhaps be an indication that it was beginning to die off.

The inner cortex consists of a large-celled tissue, and is usually the worst preserved part of the stem. The outer cortex has a strong mechanical construction, and was no doubt of much greater importance in supporting the plant than the loosely built wood. The deep fibrous bands differ from those of *Heterangium* in being united, in the tangential direction, into a regular network, with the meshes filled with a cellular tissue which becomes much dilated in stems which have undergone considerable growth in thickness (Fig. 11). This type of construction is often called "Dictyoxylon" cortex, and is distinguished from the "Sparganum"¹ cortex found in *Heterangium*, in which the fibrous strands run parallel and are seldom connected. Both forms are very common among Palaeozoic plants of various affinities, and the distinction between them is not always constant. The presence of a few layers beyond the Dictyoxylon zone has already been noticed. A conspicuous feature of the external surface of the plant is the occurrence of large and massive spines or outgrowths, which are not hairs but deep-seated emergences. They are also present on the leaves, and will be described in connection with these organs.

The Leaf-traces.—We have now to consider the course of the leaf-traces, and the changes of structure which they exhibit during their passage outwards. We will first describe the arrangement of the strands as they appear in a transverse section of the stem (Fig. 11). It is a very general rule that in the larger stems with which we are now concerned there are five leaf-traces outside the wood, in any transverse section. All five may still lie within the limits of the pericycle, the most external trace perhaps bulging it outwards. Or this trace may already be traversing the cortex on its way to enter the

¹ These terms are taken from the names of obsolete genera, once characterised by the features in question.

base of a leaf. The fact that the traces of five successive leaves are seen at once, shows that each leaf-trace must have traversed about five internodes between leaving the wood and passing out into a leaf. As the traces are all, or all but one, still within the pericycle, it follows that the outward course of the trace was at first extremely gradual, while finally it bent out somewhat sharply, to pass through the cortex and enter the leaf-base.

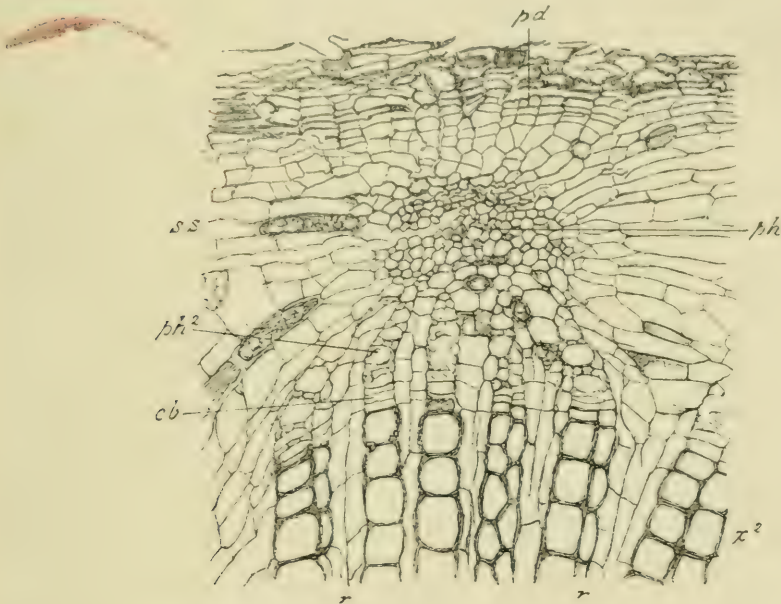


FIG. 16.—*Lyginopteris oldhamia*. Part of transverse section, from outer part of stele. x^2 , secondary wood; r , medullary rays; cb , cambium; ph^2 , secondary, ph , primary, phloem; $s.s.$, secretory sac; pd , periderm. $\times 52$. *Phil. Trans.*, W. and S. Will. Coll. 1640.

The circum-medullary xylem-strands already described are sometimes five in number like the leaf-traces outside the wood. Usually they are more numerous, some of the strands having divided to form a pair (Fig. 11). Where they are only five they alternate regularly with the external leaf-traces; where they are more numerous the same general arrangement is maintained, each pair corresponding approximately in position to an undivided strand.

Strands are often met with in the zone of secondary

wood, on their way out from pith to pericycle (Fig. 11, *l.t.*¹). It is thus manifest that the circum-medullary strands are of the same nature as the external leaf-traces, representing them, so far as the xylem is concerned, in the lower part of their course. As the circum-medullary and the external strands are continuous, the alternation of the former with the latter requires explanation. This is afforded by the comparison of successive transverse sections, enabling us to follow the exact course of a given leaf-trace.

We have seen that the phyllotaxis is normally $\frac{2}{5}$. In a good transverse section we can determine the direction of the spiral by the relative positions and changes of structure of the leaf-traces; the outermost leaf-trace is evidently destined for the next leaf above, the second outermost for the next higher leaf, and so on, the innermost trace thus belonging to the highest leaf of the five. The direction from the outermost to the next inner trace (at a divergence from it of $\frac{2}{5}$) will thus be in the ascending or *anodic* direction of the leaf-spiral; conversely, a line from an inner to the next outer trace will be in the descending or *kathodic* direction (see Fig. 11).

If we choose any one of the external leaf-traces and follow its downward course in successive transverse sections, we find that at a certain point, namely, about five internodes below its entry into the stem from a leaf, it begins to pass inwards, through the zone of secondary wood, leaving its phloem behind.¹ The xylem-strand of the trace soon reaches the edge of the pith, and, continuing its downward course, bends somewhat in the kathodic direction, until it meets the circum-medullary strand, lying in the interval between the trace in question and the adjacent one on the kathodic side (Fig. 11 and diagram, Fig. 17). The two strands then unite into one. Thus every leaf-trace on reaching the margin of the pith

¹ This is due simply to the occurrence of secondary thickening which intercalates secondary wood between the xylem and phloem.

fuses with the nearest circum-medullary strand in the kathodic direction. Conversely, if we take a circum-medullary strand lying midway between two of the external leaf-traces, and follow it *upwards*, we find that it divides into two; the larger of the two daughter-strands, which is that on the *anodic* side, curves away

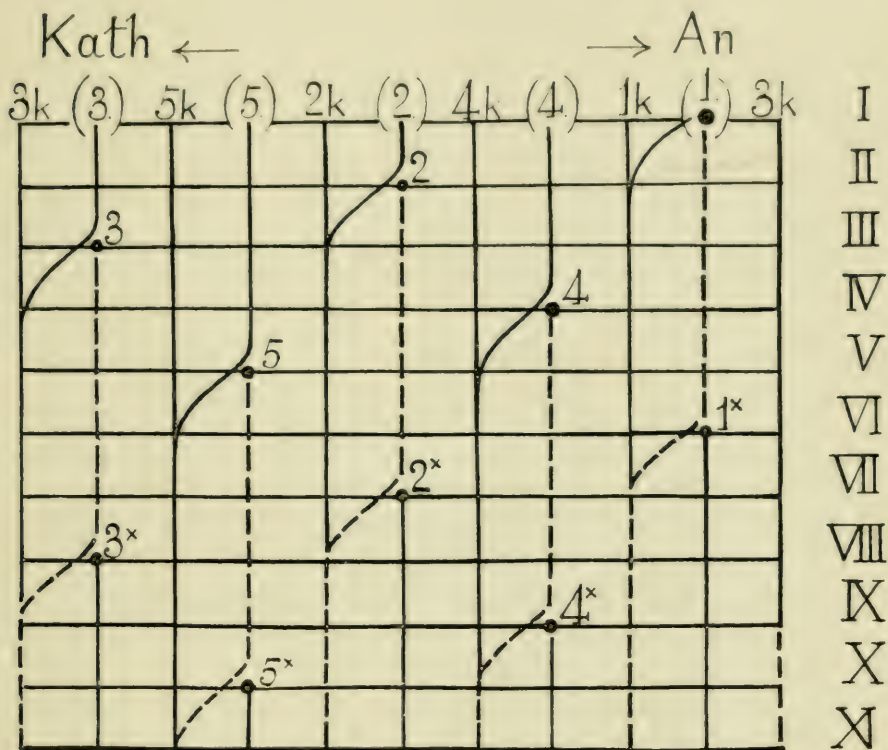


FIG. 17.—*Lyginopteris oldhamia*. Diagram of the course of the leaf-traces, showing the cylinder of bundles spread out in a vertical plane. The arrows, *Kath* and *An*, indicate the kathodic and anodic directions of the leaf-spiral. Phyllotaxis $\frac{2}{5}$. The dots 1—5 and 1^x—5^x indicate the points of exit of the leaf-traces; the numbers (1)—(5) at the top, the orthostichies. 1_k—5_k mark the reparatory strands on the kathodic side of each leaf-trace. The bundles belonging to the upper cycle (1—5) are dotted; those of the lower cycle (1^x—5^x) are shown as full lines. The Roman numerals mark the nodes. Cf. the transverse section, Fig. 11. (G. T. G.)

from the other in the anodic direction and passes out to become a leaf-trace. The other, namely, the kathodic branch of the original strand, continues its course straight up the stem, until the point is reached (five nodes higher) where it has to divide again and give off another leaf-trace, lying vertically above the former. The strands

which thus divide to give off the successive leaf-traces may be called the *reparatory* strands, as they repair the gaps left by the outgoing traces. In other words, each reparatory strand constitutes a sympodium, built up of the bases of successive leaf-traces which always diverge from the vertical in the *anodic* direction. (Diagram, Fig. 17.)

The point at which a reparatory strand divides to give off a new leaf-trace varies in different specimens, and this is why the number of circum-medullary strands in a transverse section varies. For if the division takes place relatively low down, *i.e.* some distance below the point where the new trace begins to pass out, several of the strands will be represented by pairs and the total number may rise to eight or more (see Fig. 11, where three out of the five circum-medullary strands have divided). This is usually the case in large stems. If the division only takes place high up, *i.e.* just below the emission of a new trace, the strands as seen in transverse section will either be all undivided, numbering five only, or one may have just divided, making six in all.

The significance of these details lies in the proof they afford that the entire vascular organisation of *Lyginopteris* is a leaf-trace system comparable to that of the higher plants. The special case of *L. oldhamia* is similar to that of *Iberis*, familiar to readers of De Bary's *Comparative Anatomy*,¹ if we allow for the difference in phyllotaxis, which is $\frac{5}{13}$ in *Iberis* and $\frac{2}{5}$ in our fossil. It is one of the simplest forms of leaf-trace system in plants with a spiral arrangement of the leaves, and a single bundle entering the stele from each leaf.

We have next to consider the changes of structure which a leaf-trace undergoes in its course, and here it will be most convenient to follow it from below upwards, *i.e.* from within outwards. Where a xylem-strand diverges

¹ De Bary, *Comp. Anatomy of the Phanerogams and Ferns*, Oxford, 1884, p. 237.

from its kathodic neighbour and begins to pass out, it has a single protoxylem-group, which becomes doubled as it leaves the pith (Figs. 13 and 14). Secondary thickening affects the outgoing trace, as it does the rest of the vascular ring, and in all but the youngest stems we find that the trace, on its way between pith and pericycle, has an arc of secondary wood and bast on its outer side (Fig. 11, *l.t.*¹ and *l.t.*²). When it reaches the pericycle, the zone of secondary wood closes in behind it, but for a time the trace retains its own arc of secondary tissue (Fig. 11, *l.t.*²). This gradually dies out, only the primary tissues remaining, and at the same time another change takes place, the trace dividing into two strands, side by side (Fig. 14). These changes are usually gone through in about the length of an internode, but occasionally the secondary wood and bast persist for a certain distance after the bundle has divided.

While the leaf-trace is slowly passing out through the pericycle, little further change takes place, beyond a gradual separation of the two strands. Throughout this part of its course the structure of the trace remains collateral, the phloem being limited to the external side of the xylem. Ultimately the trace begins to leave the pericycle, which for a time follows its course by an outward bulge, and then it passes rapidly through the cortex to enter the leaf-base. In traversing the cortex the two bundles of the trace are inclined to one another, converging outwards, and each assumes a concentric structure, the phloem extending all round the xylem. On entering the base of the leaf the two bundles may wholly or partially unite, or may remain distinct. In the meantime their protoxylem-groups have further subdivided, so that in the leaf-base there are often three groups in each strand.

The cortical tissues of the stem are continuous with those of the leaf-base. There is commonly a great development of sclerotic nests in the axillary region,

whereas in other parts of the stem they are mostly limited to the pith and pericycle. At a certain level a tangential band of thick-walled tissue appears immediately below the axil and is connected upwards with the Dictyoxylon cortex on the inner side of the petiole as it becomes free (Fig. 22). The leaf itself is described below (p. 42).

Young and Small Stems.—So far we have been considering the structure of a typical, full-grown stem. We often meet with stems of quite normal structure and dimensions, which are in a young condition, little or no secondary tissue having as yet been developed. In these cases there is little distinction between the circum-medullary strands and the more external leaf-traces, for there has been no intercalation of secondary wood and phloem. In such young stems the radial fibrous bands of the Dictyoxylon cortex are crowded together, for the cellular tissue between them has not yet undergone any dilatation (Fig. 18).

Apart from such examples of merely *young* stems, we meet with other cases in which the stem, though mature, is unusually small, and sometimes has a rather different structure from the specimens which we have taken as typical. In extreme cases such stems may be only about 2 mm. in diameter. In some of them the structure is essentially normal, except that the phyllotaxis appears to have sometimes been $\frac{1}{3}$ instead of $\frac{2}{5}$; sclerotic nests are often absent from the pith. Other small specimens are more remarkable, in so far that the primary xylem-strands are to a considerable extent fused laterally, so as to form a more or less continuous ring round the pith.

In the smallest stem observed, about 2 mm. in diameter when complete, the pith is obliterated, and must have been small originally. There are six circum-medullary strands close together, but not actually fused, and four leaf-traces to the exterior. It is probable that the phyllotaxis was here of the usual $\frac{2}{5}$ type. Five or six layers of

secondary wood had been formed, and the structure in all essentials is typical.

The stem of *Lyginopteris oldhamia* is now known to have often been branched, as will be described in the next section. It is possible that these minute stems may, in certain cases, represent branches of a high order, though some of them show the bases of roots, a fact which seems inconsistent with this interpretation. It

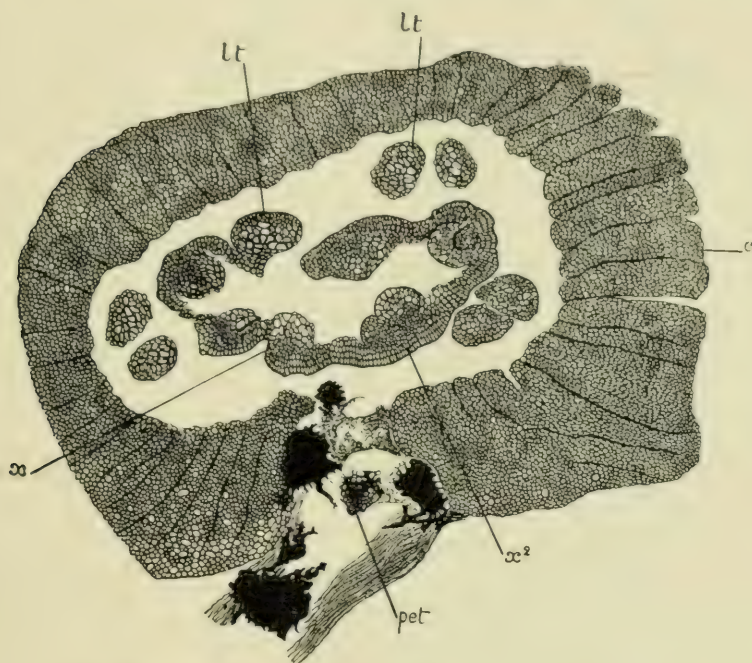


FIG. 18.—*Lyginopteris oldhamia*. Transverse section of a very young stem, at the commencement of secondary growth. x , one of the six primary xylem-strands surrounding the pith, which is not preserved; x^2 , narrow zone of secondary wood; lt , leaf-trace bundles; c , outer cortex; pet , base of petiole. $\times 11$. Will. Coll. 1144 D. (G. T. G.)

has been suggested¹ that the specimens with an almost continuous ring of primary xylem may represent the basal part of the stem, which has a similar structure in *Osmunda*, a fern presenting some anatomical analogies with the primary condition of *Lyginopteris*. But at present we do not possess the data for a positive conclusion as to the nature of the exceptionally small speci-

¹ Williamson and Scott, 1895, p. 721.

mens; it is possible that several distinct species may be involved.

Branching of the Stem.—Stems of *L. oldhamia* bearing branches were first described by Mr. James Lomax in 1902; up to that time only unbranched specimens had been met with. Since then a number of ramified stems have come to light; two such cases were described by Miss Brenchley in 1913; they are of great interest, as showing a number of branch-bearing nodes on the same axis. For anatomical details the best specimen available is one of those originally described by Mr. Lomax, from which a series of twenty-five transverse sections was prepared by him.¹

Miss Brenchley's conclusions from the specimens she investigated are:

1. That the branches were axillary.
2. That secondary and tertiary as well as primary branches occurred.
3. That the direction of the phyllotaxis of a branch was the reverse of that of the axis on which it was borne.
4. That the branching disturbed the phyllotaxis, the normal divergence of $\frac{2}{3}$ being lost in the appendages.²

It is a question whether the axillary position of the branches was constant. It will be worth while to describe the relations of branch and stem as shown in the most perfect specimen (Fig. 19), which may serve as a type of normal ramification; adventitious branching also occurred.

The diagrams (Fig. 20, I.-V.) show five transverse sections selected from the series of twenty-five, and illustrate the separation of the branch and subsequent changes. In the lowest section figured (Diagram I.) the branch (*Br*) forms a scarcely noticeable protrusion, chiefly indicated on the stele. Of the five leaf-traces,

¹ Now slides 2072-2096 in the Scott collection.

² W. E. Brenchley, "On Branching Specimens of *Lyginodendron oldhamium*, Will.," *Linnean Society's Journal—Botany*, vol. xli. 1913.

No. 1 is clearly the innermost and No. 5 the outermost. The traces do not follow the regular $\frac{2}{3}$ arrangement, for, while No. 5 is the first to pass out into a leaf, it is followed (as shown in still higher sections) by No. 4, the adjacent trace, the interval thus being $\frac{1}{3}$ instead of $\frac{2}{3}$. It will be noticed that the centre line of the branch passes



FIG. 19.—*Lyginopteris oldhamia*. Transverse section of branching stem. On the left of the figure is the base of a petiole containing two bundles (*l.t.* 5 in Diagrams I. and II., Fig. 20). The stele of the branch lies on the right of that of the main stem. \times about 4. S. Coll. 2077. From a photograph by Mr. Tams. Fig. 20, Diagram II., shows the section nest above this.

midway between the leaf-traces 2 and 3 ; it thus appears not to have been axillary, for its position does not correspond to that of a leaf, but, considering the irregularity of the phyllotaxis, this conclusion may be open to some doubt.

The five leaf-traces, in spite of their irregular succession, appear to form a single cycle belonging to the main stem. Yet we find that two of them (Nos. 2 and 3)

pass out with the branch, supplying its first two leaves. This becomes evident in the second diagram ; the intervening sections leave no doubt as to the identity of the strands. This fact sufficiently accounts for the disturbance in the phyllotaxis of the parent stem at the point of branching.

The first two leaves of the branch are thus lateral, and, judging from the similar phase of the two leaf-traces, must have been borne almost at the same level. The third leaf of the branch is abaxial and median, its leaf-trace starting from the branch-stele (Diagrams III., IV., *l.t.M*). In other words, the first two leaves of the branch are supplied by traces which pass down into the main stem, and do not join the stele of the branch until it has completely fused with that of the parent axis. The leaf-trace system of the latter undergoes a corresponding interruption.

Simultaneously with and nearly opposite the branch, a leaf (supplied by trace 5) is given off from the main stem (Diagram II.). A second leaf (supplied by trace 4) is borne at a higher level. In the meantime new leaf-traces have left the main stele ; the first of these (*l.t.A*) almost corresponds in position with the original trace 3, while the second (not figured) is on the same radius as trace 5. Thus the divergence is now $\frac{2}{5}$, and the normal phyllotaxis is being restored.

It must be specially noted that the branch receives a certain number (here five) of circum-medullary xylem-strands from the main stele, and is thus in direct continuity with the primary vascular system of the parent axis. It is this point which distinguishes the normal from the adventitious branching. Above the separation of the branch from the stem, numerous roots are given off from the latter (Diagram V.).

Several cases of adventitious branching have been observed. The essential characteristic of this form of branching is that all the primary xylem-strands remain

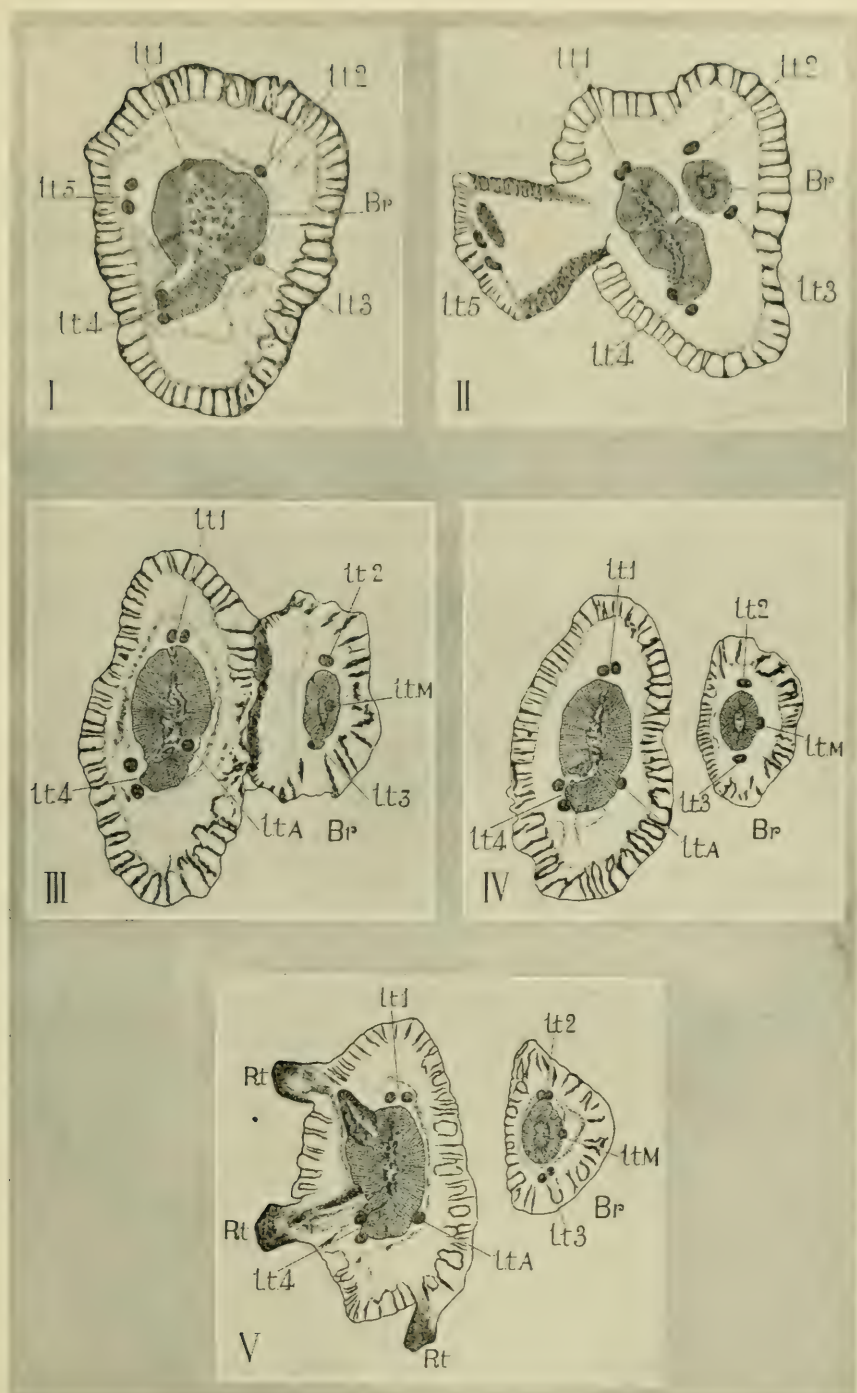


FIG. 20.—*Lyginopteris oldhamia*. Five transverse sections from a branching stem, selected from a series. *lt.1*-*lt.5*, the original leaf-traces—*lt.2* and *lt.3* pass out into the branch *Br* (see Diagrams II.-V.), and *lt.5* into a petiole (Diagram II.); *lt.A* (Diagrams III.-V.), new leaf-trace in main stem; *lt.M* (Diagrams III.-V.), new leaf-trace in branch; *Rt* (Diagram V.), roots. For full description see text. Diagram I, S. Coll. 2073; II., 2078; III., 2083; IV., 2087; V., 2090. (G. T. G.)

in the stele of the present stem ; none enter the stele of the branch. The latter is thus left without any primary xylem in its lower part, though the strands may reappear at a higher level. In such cases the first leaf-traces of the branch consist principally of secondary xylem. The structure indicates that the branches in question were somewhat late formations, perhaps due to some injury to the stem, and therefore had no share in the primary organisation of the parent axis.

The fact that for thirty-five years after the discovery of *L. oldhamia* no branching specimens were met with is significant, and may probably be an indication that the branched habit was limited to certain species included under the collective name *L. oldhamia*.

Anomalies of the Stem.—The stem of *L. oldhamia* is subject to various anomalous anatomical developments, due to the appearance of cambium in other than the normal position. These peculiarities, some of which are fairly common, are limited to individual stems, or to parts of the stem, and have no systematic significance. They are, however, of interest, as showing close analogies with anomalous structures in the stems of certain recent Dicotyledons.

The most frequent anomaly in *L. oldhamia* is the formation of a medullary cambium, usually arising just inside the primary xylem-strands and producing wood and bast with inverted orientation, the bast facing the middle of the pith. The medullary cambium is often in continuity, through the leaf-gaps, with the normal cambium, and probably this is usually the case at some point or other. In extreme instances the wood may thus become broken up into several distinct masses, each with its own ring of cambium, forming new secondary tissues all round it. Hence these isolated masses may come to simulate so many distinct steles, but this appearance is entirely due to the abnormal extension of the cambium, and has nothing to do with the primary struc-

ture. The presence of inverted medullary wood and phloem finds its analogue, for example, in the recent Bignoniaceous climber *Tecoma*, while the splitting up of the vascular ring into a number of pseudo-steles is paralleled in *Acanthophyllum* (Caryophyllaceae) and in various Sapindaceous lianes.

It occasionally happens that the parenchyma accompanying the protoxylem of the primary strands takes part in the new cambial development, and then the centripetal part of the primary xylem is carried inwards into the pith by the secondary growth. An analogous process has been observed in the recent anomalous Plumbagineous genus *Acantholimon*.

In some cases the anomalous extension of the cambium is not limited to the stele, but affects the out-going leaf-traces; one or both bundles of the divided trace may become encircled by a cambium, giving rise to a zone of secondary tissue, so that here also the whole strand simulates a stele. When this anomaly coexists with the medullary peculiarities above described, the stem may acquire a remarkably complex pseudo-polystelic structure. In addition, mere groups of sclerotic cells may become the centres of new rings of secondary xylem and phloem.

An attempt has been made to correlate these exceptional developments in *Lyginopteris* with the normal polystely of *Medullosa* and allied genera, to be described in a later chapter.¹ But the two phenomena really have nothing in common, for the steles of *Medullosa* are laid down as part of the primary structure of the stem, while the occasional appearance of stele-like masses in individual stems of *Lyginopteris* is entirely a secondary development, owing its origin to an unusual distribution of the cambium, probably called forth, in many cases, as a response to injury of the stem.

¹ W. C. Worsdell, "The Structure and Origin of the Cycadaceae," *Ann. of Bot.* vol. xx. 1906, pp. 139-143.

As Miss Brenchley has pointed out,¹ a good deal of medullary wood is frequently formed where a branch is being given off; she suggests that the anomalous tissue may help to close up the gap caused by the mass of xylem passing out to supply the shoot.

The real importance of the anomalous specimens of the *Lyginopteris* stem lies in the demonstration they afford of the wonderful plasticity which the acquirement of cambium gives to the anatomical organisation of a plant. *Lyginopteris* belonged to an early group of Seed-plants, which still retained many analogies with a Cryptogamic stock, yet it already shows, as occasional peculiarities, several of the anomalies of secondary structure which are otherwise known only among the most highly modified Dicotyledons of the present day.

The Leaf.—The best information as to the form and configuration of the leaf of *L. oldhamia* is afforded by the impressions of *Sphenopteris Hoeninghausi* (Fig. 21); the evidence of identification is given on p. 56. In sections of the petrified material the leaf is necessarily met with in a fragmentary condition; we cannot expect to find any considerable portions of the frond lying flat in the plane of section. Yet a vivid idea of the general character of the foliage can often be gained from such preparations, and all the main points are shown in them. The frond was evidently a highly compound one; all stages in its ramification, from the main petiole to the ultimate leaflets, are found. The connection between stem and petiole is shown in Fig. 22.

The impressions, as Potonié showed, prove that the principal rachis of the frond was forked, the dichotomy occurring at a point above the insertion of the lower pinnae.² Evidence of the bifurcation is also supplied by the petrified specimens, some of which show, in

¹ W. E. Brenchley, *l.c.* 1913, p. 355.

² Potonié, "Über einige Carbonfarne," ii. *Jahrbuch d. K. Preuss. Geol. Landesanstalt*, Berlin, 1890, p. 16.

transverse section, the separation of the two equal vascular bundles destined to enter the two limbs of the forked rachis. Both the primary pinnae and those of a



FIG. 21.—*Sphenopteris Höninghausi* (= *Lyginopteris oldhamia*). Frond, showing the pinna-tion and the forking of the main rachis. Reduced to $\frac{2}{3}$ nat. size. After Potonié. From *Jahrbuch d. Geolog. Landesanst. und Bergakademie*, 1890.

higher order were inserted on the rachis at a wide angle, approaching a right angle. The ultimate pinnules of the rachis bore on their slender stalk two alternating series

of small, somewhat cuneate leaflets, lobed in a varying degree. The venation of the leaflets is admirably shown in sections parallel to their surface; the veins separate from each other at an acute angle. The leaflets, in their

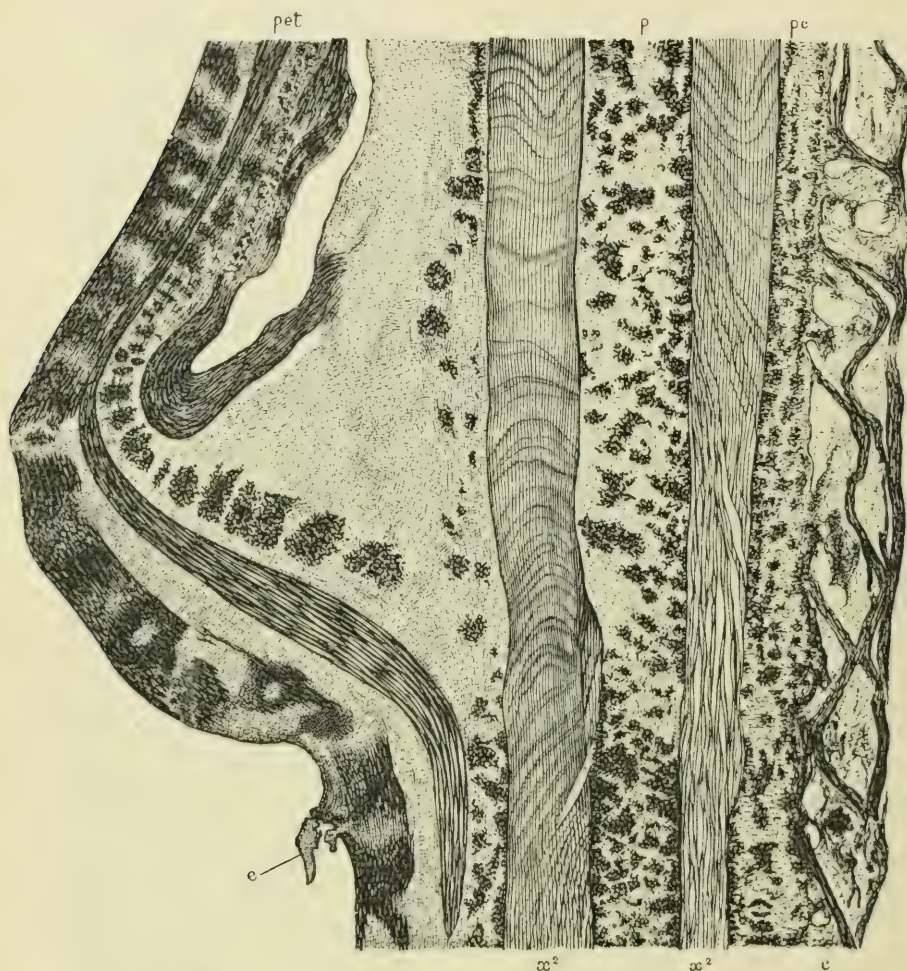


FIG. 22.—*Lyginopteris oldhamia*. Radial section of stem, passing through the base of a petiole. x^2 , wood of stem, enclosing pith; pc , pericycle; c , outer cortex; pet , petiole; the vascular bundle extends from the petiole down into the pericycle of the stem; e , cortical spines. $\times 3\frac{1}{2}$. Will. Coll. 1982. (G. T. G.)

natural condition, are somewhat conchoid, convex above and concave below (Fig. 24).

Turning now to the more strictly anatomical features, we find that in the main petiole and rachis the bundle has the form of a V or a W, with the arms pointing upwards; the W form is no doubt a preparation for the

forking of the bundle. In some cases, however, as we have seen, the two strands which enter the leaf-base from the stem remain distinct from the first. In the main branches of the rachis the V shape of the bundle is retained (Fig. 23) ; its structure is always concentric ; several protoxylem-groups are embedded in the wood towards the convex (lower) side, which of course corresponds to the outer side of the strand in the stem. The

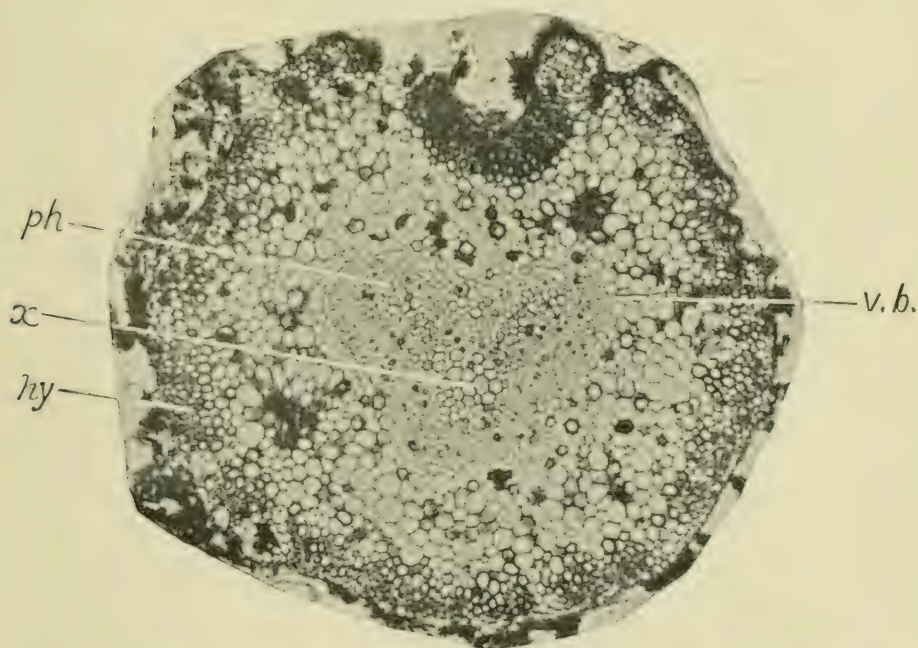


FIG. 23.—*Lyginopteris oldhamia*. Transverse section of rachis. *x*, V-shaped xylem ; *ph*, phloem, completely surrounding xylem, forming the concentric bundle *v.b.* ; *hy*, hypodermis. \times about 35. From a photograph. *Phil. Trans.*, W. and S. Will. Coll. 145.

tracheides are for the most part spiral or scalariform, but some pitted elements occur in the centripetal (upper) portion of the xylem. The Dictyoxylon cortex is continued from the stem into the petiole and principal branches of the rachis ; the inner cortex contains numerous plates of stone-cells, not unlike those in the leaf of *Heterangium* (Fig. 22). The rachis of the ultimate pinnules, which immediately bear the leaflets, has a simpler structure ; the bundle, still concentric, assumes a rounded outline, the sclerotic plates disappear, the cortical cells are

shortened, and the Dictyoxylon zone is reduced to a single hypodermal layer.

The bundles are given off into the leaflets at an acute angle, and immediately begin to branch. Both in the ultimate rachis and in the leaflet itself, each bundle is enclosed in a conspicuous sheath of relatively large cells.

In the leaflet the bundle at last loses its concentric structure and becomes collateral; the xylem may reach the sheath on the upper side, and the phloem is limited

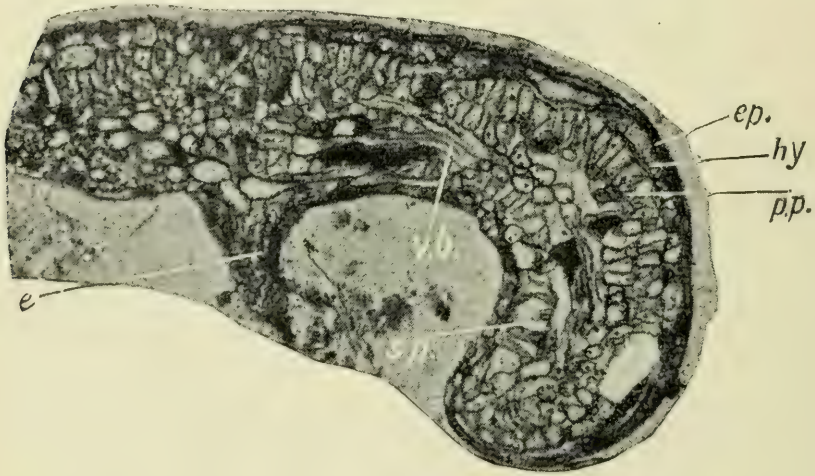


FIG. 24.—*Lyginopteris oldhamia*. Vertical section of a leaflet. *ep.*, upper epidermis; *hy.*, hypodermis; *p.p.*, palisade-parenchyma; *s.p.*, spongy parenchyma; *v.b.*, vascular bundle; *e.*, spine. \times about 70. From a photograph. *Phil. Trans.*, W. and S. Will. Coll. 1196.

to the lower part. A similar change of structure is familiar in the vascular system of the lamina in the fronds of recent Ferns.

Where the bundles of the leaflets end, the xylem is much enlarged, the tracheides becoming wider and at the same time shorter. It is interesting to recall that the same peculiarity of the bundle-endings was observed by Schimper in the leaves of the Mangrove plants of tropical seashores.¹ The leaflets are relatively thick, with their lobes incurved towards the lower surface (Fig. 24).

¹ A. F. W. Schimper, *Die indo-malayische Strandflora*, Jena, 1891, p. 14, Plate iv. Fig. 3.

Beneath the upper epidermis is a hypodermal layer of rather thick-walled cells, a feature characteristic of xerophytic or halophilous plants, and next comes a well-marked palisade tissue, with cells vertically elongated, as is usual in this position. Towards the lower surface the cells of the mesophyll are shorter and less closely packed, forming the spongy parenchyma. Stomata, somewhat depressed beneath the surface, are found in the lower epidermis.

The structural features of the frond of *Lyginopteris* are on the whole those which characterise the leaves of plants inhabiting either a dry situation or one in which the roots are exposed to salt water.

All parts of the leaf are studded with spines or glands, to which we will now turn our attention.

The Glandular Spines.—Spines are present on all the organs of the plant except the roots. The stem, the petioles, the rachis of all orders, and the leaflets, especially on their lower surface, are studded with these outgrowths. On the rachis they are remarkably conspicuous, ranged in long parallel rows. They densely clothe the youngest branches and leaves, forming a protection to the bud. Such immature, spine-clad buds, perhaps arrested in development, are sometimes found in the axils of the leaves.

The spines are massive, deep-seated organs, and are therefore not of the nature of hairs. They have no vascular supply, and fall technically under the head of "emergences." In extreme cases they may reach a length of something like $\frac{1}{8}$ of an inch (3 mm.); they frequently exceed 2 mm., but others are quite short. The spine is usually flask-shaped, with a broad base tapering to a narrow neck (Fig. 25), but the form is very variable.

A well-developed spine consists of a thick-walled epidermis (occasionally showing stomata) overlying a few layers of fibrous elements, which enclose a core of

thin-walled cellular tissue. A spine is commonly seated astride of a parenchymatous band of the outer cortex, the fibrous tissue of the spine joining on to the adjacent fibrous ribs of the supporting organ and its cellular core to the parenchyma between (Fig. 32). In the smaller spines the epidermis alone has thickened cell-walls.



FIG. 25. — *Lyginopteris oldhamia*. Vegetative gland, showing well-preserved secretory tissue filling the head. The depression on the right of the stalk is a stoma. \times about 60. S. Coll. 447. From a photograph by Mr. L. A. Boodle, F.L.S. (*Phil. Trans.*, Oliver and Scott.)

It appears that all the spines terminated, when complete, in a glandular head. At one time a distinction was drawn between spines and glands, but a re-investigation has shown that wherever the end of a spine is completely preserved, it is crowned by a glandular body. The latter, it is true, has often perished, perhaps normally, perhaps as the effect of decay.

The glandular head is a round or oval body, ranging from 120μ to 400μ in diameter. The interior is filled by a mass of small, angular, or rounded cells, which no doubt constituted the secretory tissue. The free outer wall is composed of a layer of thin, tabular cells, the wall becoming thicker at the sides, and passing over below into the outer tissues of the spine

(Fig. 25). In some cases the secretory tissue has more or less completely broken down, leaving the head nearly or quite empty (Fig. 32).

The glandular bodies are borne on spines of all sizes, and also sometimes occur in a sessile position. In some cases the glandular head is large relatively to the stalk

or spine, in others the reverse is the case. Specially large glands, often with a comparatively slender stalk, appear to characterise particular forms of the plant, possibly distinct species. In such cases, where the gland is large in proportion to the stalk or actually sessile, one may suppose that secretion was the sole function of the organ. But where the spine is well developed and the glandular body relatively small, it is evident that there was a double function. The secretory activity may well have been only transitory, while the spine persisted, either as a protective organ or perhaps as an aid in climbing, if such was the habit of the plant.

The glandular spines of *Lyginopteris oldhamia* have twice played an important part in the reconstruction of the plant from its fragmentary remains. The similar "emergences" occurring on stem and leaf assisted Williamson in recognising his "*Rachiopteris aspera*" as the petiole of *Lyginopteris*.¹ At a later date (1903) it was by means of the glands on the cupule that the seed of *Lyginopteris* was first identified (see p. 63).

In addition to the glands or spines, true hairs, composed of a single row of cells, are also formed.

The Roots.—The stem of *L. oldhamia* bore large numbers of adventitious roots, once described as a separate plant, under the name *Kaloxylon Hookeri*. It seems that the roots must have been aerial,² for they are borne on the stem among the bases of the foliage-leaves and above the insertion of branches (see above, p. 38), that is, on parts which could scarcely have been near the base. They also grow out from the stem on all sides equally; it is therefore unlikely that the stem was a creeping one, and indeed its obviously radial organisation points to a more or less erect habit; it is, however, not unlikely that its lower part may have often been submerged under the waters of the swamp.

¹ Williamson, *l.c.*, Part xvii. *Phil. Trans. Royal Soc.* 1890, B, p. 91.

² This suggestion was originally due to Mr. James Lomax.

The roots branched freely, and many of the rootlets must, it seems, also have been aerial, for they sometimes arose from the base of the root, where it had scarcely emerged from the parent stem (Fig. 26).

The position of the roots on the stem shows no direct relation to that of the leaves, but there was an indirect relation, for the primary wood of the roots is commonly inserted on the xylem-strands round the pith, and we

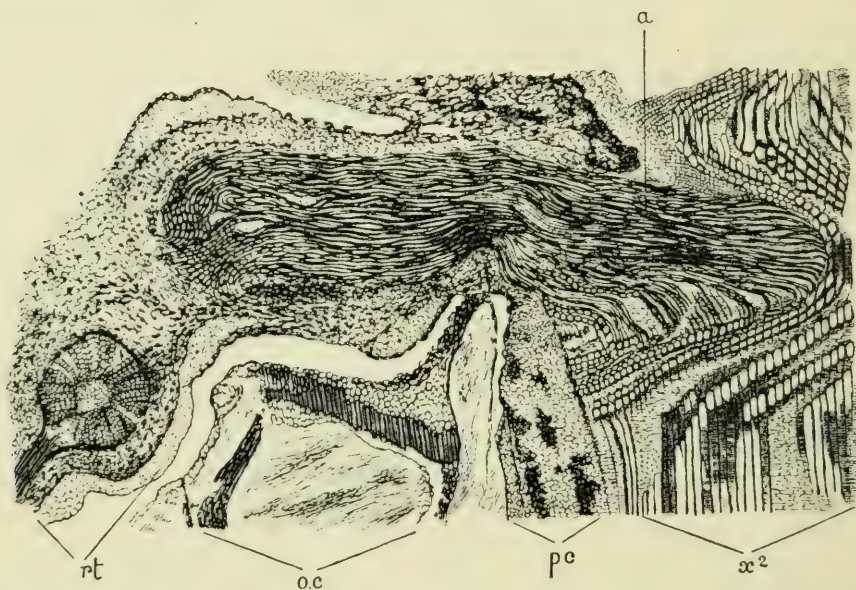


FIG. 26.—*Lyginopteris oldhamia*. Part of radial section of stem, showing an adventitious root, which is so curved as to be seen partly in longitudinal, partly in transverse section. x^2 , secondary wood of stem; pc , pericycle; $o.c.$, outer cortex; a , connection between root and wood of stem; rt , root, in transverse section, showing tetrarch structure, and giving off a rootlet. $\times 9$. S. Coll. 466. (G. T. G.)

have seen that the latter alternate with the leaf-traces (p. 29). The roots are sometimes borne on the stem in short vertical rows, and often several are inserted at about the same level (see Fig. 20, Diagram V.). The connection of a root with the stem is shown in Fig. 26.

The roots are among the best-preserved organs of the plant, and almost every point in their structure and development is clear. The main roots reach a diameter of about 7 mm., while the ultimate rootlets are quite minute, less than 0.3 mm. in thickness. The rootlets are

extremely abundant in many coal-balls, penetrating into all kinds of vegetable debris, and even into each other, just like the Stigmarian rootlets.

All the larger roots were capable of secondary growth in thickness, but the finer rootlets usually remained in the primary condition. We will first consider the structure of a main root at the stage before secondary thicken-

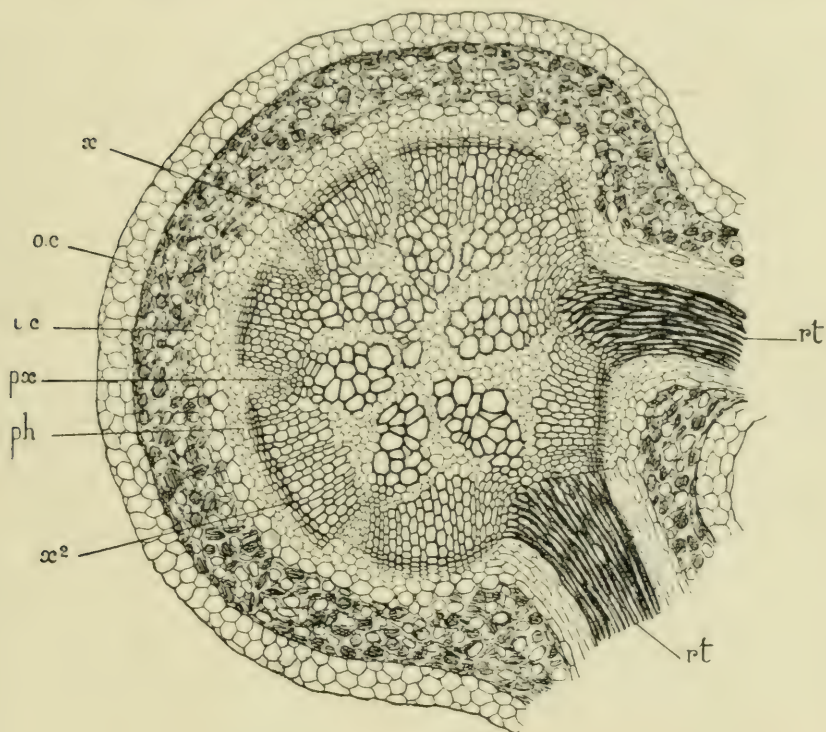


FIG. 27.—*Lyginopteris oldhamia*. Transverse section of root, somewhat diagrammatic. *px*, one of the protoxylem-groups; *x*, the heptarch primary wood; *x*², secondary wood; *ph*, phloem; *i.c.*, inner cortex; *o.c.*, outer cortex; *rt*, rootlets, opposite two protoxylem-groups. $\times 24$. Founded on S. Coll. 448. (G. T. G.)

ing had begun. Such a root consists of a stele of moderate size, surrounded by a wide cortex, bounded externally by a conspicuous peripheral zone, usually two cells thick.

In the principal roots the stele ranges from tetrarch to octarch structure. The specimen figured is heptarch (Fig. 27). The structure is perfectly typical; the arms of the xylem are prominent, each terminating on the outside in the small elements of the protoxylem, which are seen

in longitudinal section to be spiral tracheides. The more central elements of the wood are pitted like those of the stem. There is no pith, but a certain amount of conjunctive tissue is present among the tracheides. The phloem-groups alternate regularly with the protoxylem-angles of the wood, lying in the depressions between them. The stele is bounded in the usual way, by a pericycle and endodermis. Beyond the endodermis comes the broad zone of cortex, consisting of rather large cells, loosely packed, so as to leave considerable intercellular spaces between them. Numerous "secretory sacs," with dark contents, are scattered through the cortex. Lastly, we reach the peripheral zone, consisting of two or three layers of large cells, more resistant than those of the cortex. This zone has much the appearance of a velamen, which is quite what one would expect to find on an aerial root, but no markings on the walls have been detected. Nothing exterior to this zone appears to have existed, so we may regard the outermost layer, at any rate, as epidermal.

Such is the structure of a young root before secondary thickening had set in. The cambium was first formed in the conjunctive tissue lying on the inner side of each of the phloem-groups, in the intervals between the prominent protoxylem-angles. Subsequently the isolated secondary arcs became united, by divisions taking place in the pericycle outside the protoxylem-groups, so that the cambium and secondary tissues formed a continuous but wavy ring, which, as growth proceeded, became filled out into a circle. In the thickened root a principal ray lies opposite each protoxylem-angle, dividing the secondary zone into wedges, corresponding to the original phloem-masses (Fig. 27). These rays, however, may become broken up by intercalated rows of tracheides. It does not appear that the cortex was ever cut off by periderm. It will be seen that the secondary growth, like the primary structure, is altogether typical

and comparable in every respect to that in the root of a Gymnosperm or Dicotyledon.

The branching of the root is equally normal. The rootlets arose exactly opposite the protoxylem-strands of the parent root, and were manifestly endogenous in origin (Fig. 27).

The finer rootlets are commonly diarch. It will be remembered that van Tieghem showed that there is a constant difference between Phanerogams and Vascular Cryptogams in the orientation of the xylem-plate of a diarch rootlet; in the former it is vertical, in the latter horizontal, with reference to the axis of the parent root.¹ Prof. F. E.

Weiss has made the interesting discovery that in *Lyginopteris*, the

plane of the xylem plate of the rootlet is vertical² (as shown in Fig. 28), so that in this respect, as in the fructification, *Lyginopteris* shows itself to have been a Seed-plant and not a Cryptogam.



FIG. 28.—*Lyginopteris oldhamia*. Tangential section through cortex of small root, bearing a diarch rootlet, which is cut transversely. The xylem-plate of the rootlet is vertical; it appears as a row of clear cells in the middle of the little stele. \times about 200. Manchester Coll., R. 1025, 1. From a photograph by Mr. W. Tams.

¹ van Tieghem, *Traité de botanique*, Paris, 1891, pp. 702, 705.

² Weiss, "The Root-apex and Young Root of *Lyginodendron*," *Manchester Memoirs*, vol. lvii. 1913.

Even the smallest rootlets can be identified by means of the secretory sacs in the cortex and the double peripheral zone. The rootlet has a diarch xylem-plate, with the phloem-groups on either side ; a single-layered pericycle and endodermis are present. The latter consists of cells, which generally fit on to those of the cortex outside, but not to those of the pericycle within. Thus the endodermis is, as it should be, the innermost layer of the cortex ; the dark marks on some of its radial cell-walls may indicate the "Casparyan strips." The cortex was evidently a somewhat lacunar tissue ; numerous secretory sacs are present. The double peripheral layer is conspicuous ; the cells of the two rows do not correspond, so they may be of diverse morphological origin. No root-hairs have been observed ; they would probably be absent in a plant such as *Lyginopteris*, which almost certainly lived in a watery habitat.

It is remarkable that, while the structure of the stem is peculiar and unfamiliar among recent plants, that of the root is perfectly typical, and indeed might be used to illustrate the most ordinary features of root-organisation in the higher plants. This fact bears out the opinion that the root, in the chief outlines of its structure, is a conservative organ, which has come down to us with little change, from very early stages in the evolution of vascular plants.

Not only are the finest details of the root-structure in *Lyginopteris* often well preserved ; there are also several good examples of the actual apex or growing point of the root. Such specimens were first discovered by Dr. Marie Stopes and Mr. Watson,¹ and were more fully investigated by Prof. F. E. Weiss.² The root-cap is evident ; a section, which seems to be nearly median, shows the plerome in the central region as well as the

¹ Stopes and Watson, "On the Distribution and Origin of Coal-balls," etc., *Phil. Trans. Royal Soc. Series B*, vol. 200, 1908, p. 173.

² Weiss, *l.c.* 1913.

young cortex, further to the outside. The question whether there was a single apical cell or an initial group must, however, be left open ; Prof. Weiss inclines to the former view.

Habit.—We have already described the principal features in the structure of all the vegetative organs of *Lyginopteris oldhamia*. We may now attempt a reconstruction of the plant, so as to gain some idea of its habit, before going on to consider the subject of the organs of reproduction (see below, p. 63).

The stem must have been a comparatively slender one, of great length compared with its diameter. This appears to be proved by the length of the internodes (about an inch or so), and by the fact that every piece of stem shows, on the average, the traces of ten successive leaves (five traces outside the vascular ring and five or more around the pith). As the great majority of the specimens show no signs of any approach to the apex or base, it seems clear that they represent fragments of very long stems, bearing a large number of leaves. Although the stem was well constructed mechanically, thanks principally to the sclerenchymatous network of the outer cortex, it may be doubted whether an axis of such length and such slender proportions, bearing numerous leaves of large size, could have supported itself unaided in the vertical position. Yet the plant shows complete radial symmetry, and could not well have been of prostrate habit. It is not unlikely that *Lyginopteris oldhamia* was a climbing plant of the "scrambler" type, a suggestion which is confirmed by the presence of spines on the stem, and on all parts of the compound leaves. These spines may well have been organs of attachment, enabling the plant to cling to the trees or shrubs which supported it, just as we see in the recent Fern *Davallia aculeata*, where, however, it is only the frond, and not the stem that climbs. On the other hand, a comparison has been suggested with the tall, erect species of *Todea*, such as *T. australis*.

The evidence for the identification of the foliage of our fossil with *Sphenopteris Höninghausi* is now conclusive. The agreement is exact in the venation, form, and size of the leaflets, and in their conchoid curvature, in the mode of branching of the rachis, the presence of spines on all the parts, and the reticulated cortex of the petiole. Further, casts were figured by Zeiller, which agree closely with the stem of *Lyginopteris*, and at the same time bear the foliage of *Sphenopteris Höninghausi*.¹ The leaves of this species, which are very perfectly preserved as impressions, from the same horizon to which the specimens of *Lyginopteris oldhamia* belong, were of large size, and highly compound—tripinnate or more, with the main rachis forked, as already mentioned (see Fig. 21). There are various other species of Carboniferous Fernfronds of very similar habit, and it is quite possible, as Zeiller² suggested, that all may have belonged to stems of the *Lyginopteris* type.

The arrangement of the *Sphenopteris* leaves on the *Lyginopteris* stem, in $\frac{2}{5}$ phyllotaxis, has already been mentioned, and appears to agree with that of the specimens described by Zeiller. In the drawing³ reproduced in the Frontispiece, an attempt has been made to give a restoration of the plant, as it would have appeared in nature. The slender stem (of which only the lower part could be included in the figure) is shown somewhat inclined, to indicate that it was probably supported by other plants. Its surface bears the characteristic spines, and shows traces of a reticulated cortical structure. The arrangement and form of the large, highly compound leaves are known, from the evidence given above, to be

¹ Zeiller, *Bassin houiller de Valenciennes*, p. 84, Plate vi. Fig. 1, 1886. See also Kidston, "Microsporangia of Pteridospermeae," *Phil. Trans. Roy. Soc. B*, vol. 198, 1906.

² Zeiller, "Obs. sur quelques fougères des dépôts houillers d'Asie Mineure," *Bull. Soc. Bot. de France*, vol. xiv. p. 195, 1897.

³ Prepared, according to my instructions, by Mr. J. Allen, a skilful botanical artist.

essentially true to nature, the lamina of the leaf having been copied from that of *Sphenopteris Höninghausi*. The forking of the main rachis, however, does not come out in the figure. The position of the branching adventitious roots on the stem is correct; some of them were borne on aerial parts of the stem, as shown in the figure, while others were, no doubt, entirely buried in the soil. The drawing was made before the discovery of the branching of the stem, which we now know to have occurred freely in many specimens (p. 36).

The pendulous, tufted bodies shown, in Fig. 1 (Frontispiece), on parts of the foliage, are intended to represent the lobed cupules, discovered by Stur in another species, and now known to have enclosed the seeds.

LYGINORACHIS

This genus has been suggested by Dr. Kidston for isolated petioles, showing a structure closely similar to that of the petiole in *Lyginopteris*. In the absence of any further evidence, we cannot refer them with certainty to that genus, and the new provisional name *Lyginorachis* thus serves a useful purpose. Two species are at present known, both of Lower Carboniferous age.

Lyginorachis Papilio, Kidston

There is a certain amount of evidence for the occurrence of the genus *Lyginopteris* in Lower Carboniferous rocks, the strongest case, perhaps, being that of *Calymmatotheca Stangeri*, Stur (see p. 71), which was almost certainly a *Lyginopteris*. In the absence, hitherto, of any evidence from Lower Carboniferous specimens showing structure, considerable interest attaches to a petiole, *Lyginorachis Papilio*, discovered by Dr. Kidston in the Calciferous Sandstones of the Tweed, for its characters are closely similar to those of a typical *Lyginopteris* petiole, such as that of *L. oldhamia*.

The single specimen was found at Norham Bridge, on the Tweed, in the Cement Stone group of the Calcareous Sandstone Series. It has hitherto been undescribed, and the discoverer kindly permits me to give some account of the fossil here.

The petiole measures about 8 by 6 mm. in diameter. In form it is somewhat flattened on one side (no doubt the upper surface) and convex on the other. It contains a single, very large vascular bundle, U-shaped in transverse section, with the concavity directed towards the upper surface. The resemblance to the wings of a butterfly suggested the appropriate specific name. The inner cortex contains sclerotic nests, and the outer zone probably has a Dictyoxylon structure.

The bundle was no doubt concentric, for such remains of the phloem as are preserved occur on all sides. The convex side of the xylem is irregularly indented, but this appears to be due in part to decay, for the irregularity varies in degree in different sections. Groups of small elements, presumably the protoxylem, are embedded in the wood near its convex side, just as in the petiolar bundle of *Lyginopteris oldhamia*. In the present case, however, they are more numerous than in the Coal-measure species, the number in *L. Papilio* being about ten. A small strand, with its protoxylem directed outwards, is being given off from each extremity of the main bundle, just as in *L. oldhamia*, where similar strands pass out from the rachis into the pinnae.

Longitudinal sections show that most of the tracheides bear multiseriate bordered pits; scalariform elements are few, and are probably limited to the neighbourhood of the protoxylem-groups. In the petiole of *L. oldhamia* the proportion of scalariform to pitted tracheides is greater.

The inner cortex consists of a short-celled parenchyma, in which the sclerotic nests are embedded. The latter form somewhat flattened groups or plates, transversely

placed, and of no great extent. In all respects the agreement with the corresponding zone of the petiole in *L. oldhamia* is complete.

The outer cortex, so far as can be judged from the somewhat imperfect tangential sections, is of the Dictyoxylon type, the fibrous strands forming a network, as in *Lyginopteris*, and not running parallel, as in *Heterangium*.

It will be observed that *Lyginorachis Papilio*, both in general anatomical configuration and in the detailed structure of the various tissues, agrees very closely with the petiole of a *Lyginopteris* such as *L. oldhamia*. The differences noticed, in the greater number of protoxylem-groups and the smaller proportion of scalariform tracheides, appear to be only of specific value. The agreement with *Heterangium* is decidedly less close. In *H. Grievii*, the only species which is readily comparable, the form of the bundle in transverse section is much simpler, the sclerotic nests are in the form of more extensive flat plates, and the outer cortex is of the Sparganium, not of the Dictyoxylon type.

It may seem, then, that we should be justified in referring the fossil to the genus *Lyginopteris*, as the petiole of some unknown Lower Carboniferous species. The genera *Lyginopteris* and *Heterangium*, however, are so closely connected, especially through the intermediate forms discovered by Dr. Kubart, that we cannot draw any perfectly certain conclusion from the petiole alone. It is therefore best to leave the Tweed specimen in the provisional genus *Lyginorachis*, but it may safely be stated that *Lyginorachis Papilio* has more in common with the petiole of a *Lyginopteris* than with that of any other known genus.

A second species, *Lyginorachis Taitiana*, Kidston, from the Carboniferous Limestone Series of Lanarkshire, and therefore somewhat younger than *L. Papilio*, differs from that species in the form of the bundle and some

other details, but is equally suggestive of the petiole of a *Lyginopteris*.

Other Species of Lyginopteris

Additional species of the genus have been briefly recorded by Dr. Kubart, from the Ostrau Beds of Upper Silesia. While *L. lacunosa* appears to be essentially of the *L. oldhamia* type, others, such as *L. tristicha*, are peculiar in so far as the primary xylem-strands are united to form a more or less continuous ring round the pith. The ring is enlarged to form a distinct strand at the points where a leaf-trace is to be given off. In *L. tristicha* there are commonly three of these prominent xylem-strands, in other species more.¹ The species with a fused primary xylem are described as more complex than those with separate strands, but further details must await the fuller investigation which Dr. Kubart is undertaking.

THE ANATOMICAL CHARACTERS OF THE LYGINOPTERIDEAE

At present only the two genera, *Heterangium* and *Lyginopteris*, are definitely referred to the Lyginopterideae; the possible relation of Dr. Gordon's genus *Rhetinangium* to the family will be considered in the next chapter.

Heterangium and *Lyginopteris* have the following anatomical points in common :

Mesarch xylem-strands in stem, petiole and rachis.
Leaf-traces collateral in stem, concentric in petiole and rachis.
Normal secondary growth in thickness in stem and root
(apart from individual anomalies in certain stems of
L. oldhamia).

¹ Kubart, *l.c.* 1914; also 1908 and 1911.

Tracheides (apart from the protoxylem-region) pitted with multiseriate bordered pits.

Sclerenchyma much developed, both in the form of hypodermal ribs, and of sclerotic plates or nests in the more internal tissues.

Adventitious roots numerous; the relatively main roots triarch to polyarch, the rootlets diarch.

As not strictly anatomical characters may be added the radial symmetry of the stem, with spirally arranged leaves, and the highly compound foliage, of the Sphenopteroid type, where its form is known.

The structure of the stem, as we have seen, ranges through various intermediate stages, from the protostele of *Heterangium* to the eustele¹ of *Lyginopteris oldhamia*. That the latter is an approach to the structure of the higher Seed-plants is obvious; the discussion of this relation will be postponed to a later stage, when we have gathered more data, but at this point a word may be said on the question of the relation of Lyginopterideae to the Ferns. *Heterangium*, assuming that it bore seeds (p. 80), is the best-authenticated case of a Seed-plant with a protostele—a remarkable combination of characters. As has already been mentioned (p. 8), the stele of *Heterangium* has certain points in common with that of the simpler *Gleichenias*. In like manner, the anatomy of *Lyginopteris* has been compared with that of *Osmunda*, and so far as the primary structure of the stem is concerned, there is no doubt a certain resemblance in the ring of collateral, in part mesarch, vascular bundles.

But such comparisons with recent Ferns are at best only analogies. Though both *Gleicheniaceae* and *Osmundaceae* have a fairly long geological history, we may say with some confidence that neither group as we now

¹ Eustele is the late Mr. Brebner's term for a central cylinder with a ring of collateral bundles surrounding a pith and surrounded by a pericycle. It is more precise than siphonostele.

know it had come into existence at the time when *Heterangium* and *Lyginopteris* flourished. The oldest known Osmundaceae, of Permian age, had a stem-structure quite different from that of *Lyginopteris*. It is impossible to suppose that there was any affinity between the Lyginopterideae and the late or recent Ferns which we arbitrarily compare with them. It is more to the purpose to inquire whether the family shows any relationship, as indicated by the anatomy, with contemporary groups of fossil Ferns. The answer must be in the negative. The classes of Palaeozoic Ferns of which the structure is known are the Primofilices¹ and the *Psaronii*. The Primofilices include, for anatomical purposes, the Botryopterideae and the Zygopterideae;² the former have a simple, solid protostele, the latter a protostele more or less complicated by the differentiation of an internal xylem distinct from the outer zone of wood. In neither family is there any resemblance to the *Heterangium* type of protostele, while the leaf-traces throughout are on a totally different plan from those of the Lyginopterideae.

The *Psaronii*, complex solenostelic or polystelic Ferns, apparently of Marattiaceous affinities, have nothing in common with Lyginopterideae beyond a certain similarity in the polyarch roots, a point on which no great stress can be laid.

There is, in fact, nothing in the anatomical evidence to indicate a relationship between the Lyginopterideae and any known family of Palaeozoic Ferns. It is true that they resemble the Ferns more than any other class of Vascular Cryptogams, but there is no proof, in the present state of our knowledge, of any direct genetic connection between the two groups. For the moment, the Lyginopterideae, in some anatomical respects the

¹ The name given them by the late Dr. Newell Arber, who intended it to designate the Ferns most characteristic of the Primary Rocks.

² Both families may be classed under the common name Botryopteridaceae. See Vol. I. Chap. IX.

most primitive known representatives of the Seed-plants, must stand by themselves.

THE FRUCTIFICATION OF THE LYGINOPTERIDEAE

In considering the important subject of the reproductive organs of the family, it will be best to begin with *Lyginopteris oldhamia*, the plant in which we have the most direct evidence, both for the seeds and the pollen-sacs.

The Reproduction of Lyginopteris oldhamia

The Seed.—Up to the year 1903 our knowledge of this type was practically limited to the vegetative organs. Any previous observations, bearing on the mode of reproduction, were still of uncertain significance; there was nothing to show whether *Lyginopteris* was a Fern or a seed-bearing plant. Definite and decisive evidence was first obtained when Prof. F. W. Oliver succeeded in identifying an unassigned seed as belonging to *Lyginopteris oldhamia*, by means of the glands borne on its outer envelope. The seed in question had been named by Williamson (in MS.) *Lagenostoma Lomaxi*: the genus *Lagenostoma* was founded by him, but he had left this species undescribed.¹

Lagenostoma Lomaxi is a barrel-shaped seed, of rather small size compared with many other Palaeozoic seeds, the extreme dimensions reaching 5.5 mm. in length by 4.25 mm. in maximum diameter. It is enclosed in an outer husk or capsule, which completely enveloped the seed when young (Fig. 29) though it was no doubt open at maturity (see Fig. 30, from a model). In fortunate

¹ Oliver and Scott, "On *Lagenostoma Lomaxi*, the Seed of *Lyginodendron*," *Proc. Roy. Soc.* vol. lxxi. 1903; "On the Structure of the Palaeozoic Seed *Lagenostoma Lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodendron*," *Phil. Trans. Roy. Soc. B*, vol. 197, 1904.

cases the cupulate seed is found still attached to its stalk or pedicel: both pedicel and cupule are studded with



FIG. 29.—*Lagenostoma Lomaxi*. Longitudinal section of a small seed, invested by the lobed cupule, which bears numerous glands. Micropyle and pollen-chamber well shown; chalazal tissue displaced. From a photograph by Mr. Boodle. Oliver and Scott, *Phil. Trans.* \times about 15. Will. Coll. 1931, A.



FIG. 30.—Restoration of the seed of *Lyginopteris* (*Lagenostoma Lomaxi*), from a model by Mr. H. E. Smedley. The seed is shown surrounded by the open glandular cupule.

the capitate glands by the help of which the relation of the seed to *Lyginopteris* was first established (Figs. 29

and 30). The glands, though occasionally sessile, are usually borne each on a stout, multicellular stalk. The cavity of the head is, as a rule, empty, and the whole structure is identical with that of the well-known glands on the vegetative organs of *Lyginopteris oldhamia*, at a stage when the secretory tissue had perished. (Compare Fig. 31 from the cupule of *Lagenostoma Lomaxi*, with



FIG. 31.—Capitate gland on the cupule of *Lagenostoma Lomaxi*. $\times 70$. Oliver and Scott, *Phil. Trans.* S. Coll. 558.



FIG. 32.—Capitate gland on the petiole of *Lyginopteris oldhamia*. $\times 70$. Oliver and Scott, *Phil. Trans.* Univ. College Coll. M 11, c.

Figs. 31 and 32 from photographs by Mr. Boodle.

Fig. 32 from a petiole of *Lyginopteris oldhamia*.) No other fossil plant is known with glands of this kind, and, considering the close and constant association of the seed with the stem and foliage of *L. oldhamia*, we are well justified in assigning the seed to this plant. The conclusion drawn from the identity of the glands is supported by further structural evidence, as will be seen below.

The cupule has been compared in its general form to the husk of a hazel nut, and more especially to the

glandular husk of the Eastern species *Corylus Colurna*; it was ribbed in its lower, gamophyllous part, and divided into free lobes above (see Figs. 30 and 35). The cupule was borne on the pedicel immediately below the base of the seed, which it surrounded without being in any way attached to it (see diagram, Fig. 34).

The pedicel was traversed by a single vascular strand, of concentric and mesarch structure. Before entering the chalaza of the seed this strand gave off a number of

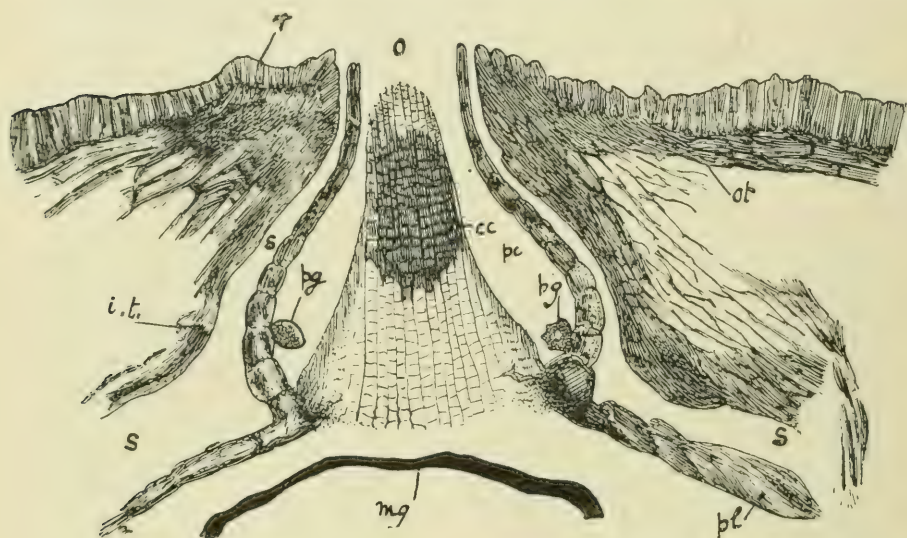


FIG. 33.—*Lagenostoma Lomaxi*. Apex of seed in median longitudinal section through micropyle. *r*, palisade-layer; *ot*, outer; *it*, inner wall of canopy (integument); *s*, space between canopy and nucellus; *p.c.*, cavity of pollen-chamber; *o*, its orifice; *c.c.*, central column of pollen-chamber; *p.g.*, pollen-grains; *pl*, part of nucellus supporting pollen-chamber; *mg*, membrane of megaspore. \times about 50. After Oliver. Univ. College Coll. R 1.

bundles (probably nine or ten) into the cupule; the cupular bundles were branched and appear to have been collateral and mesarch. There is, in fact, a detailed agreement in structure between the strands of the pedicel and cupule on the one hand and those of the rachis and leaflet of *Lyginopteris*, on the other. Thus all the evidence goes to show that the pedicel and cupule were of a foliar nature. Multicellular hairs were borne on the young cupule, as they were on young vegetative parts of *Lyginopteris*.

We now come to the seed itself, which was orthotropous and, broadly speaking, of a Cycadean type; its symmetry is perfectly radial (Fig. 35). The single integument has a somewhat complex structure, and, while entirely free from the cupule, is completely adherent to the nucellus, except in the apical region (Fig. 34).

The central strand of the pedicel, after giving off the cupular bundles, passes straight up, and becomes the chalazal bundle of the seed; in this region it is embedded in a mass of thick-walled strengthening tissue. The chalazal bundle then breaks up into about nine peripheral strands, which traverse the whole length of the integument (Figs. 34 and 35). In its upper part, where it becomes free from the nucellus, and forms the micropyle,

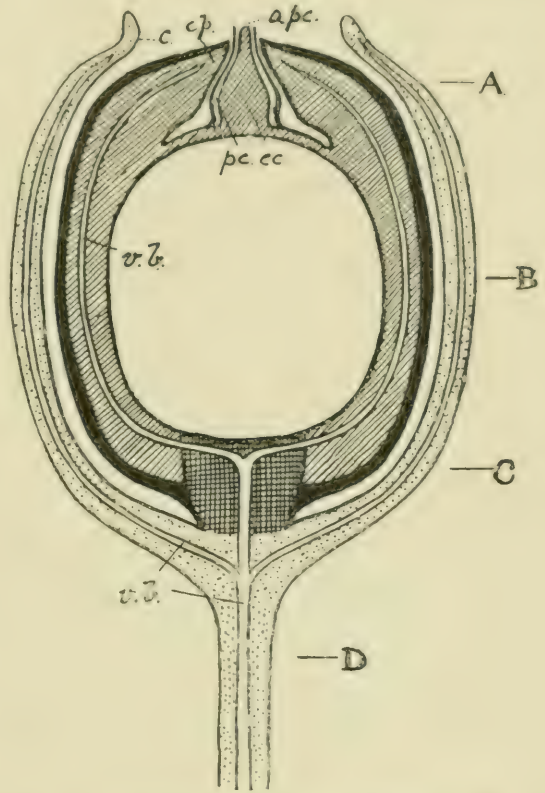


FIG. 34.—*Lagenostoma Lomaxi*. Diagram of seed in median longitudinal section. *c*, cupule; *v.b.*, vascular bundles of pedicel, cupule, and integument; *cp*, canopy of integument; *p.c.*, cavity of pollen-chamber; *c.c.*, central column; *o.p.c.*, orifice. A, B, C, D, planes of the transverse sections in Fig. 35. After Oliver.

the integument expands into a chambered "canopy," a ring of nine loculi, separated from each other by thick partitions, and originally filled by a delicate tissue, which has usually perished (Fig. 35, A). Into each of these loculi one of the nine vascular strands of the integument enters, and there terminates. The canopy, with its ample vascular supply, probably represents an apparatus

for water-storage, serving perhaps, as has been suggested, to provide the necessary liquid for pollination by means of a "drop-mechanism." The outer layer of the in-

tegument has a columnar or palisade-like structure (Figs. 33 and 36); there is some evidence that the secretion of mucilage took place from this layer, as is so often the case with the seeds of living plants.

As in recent Cycads and in the Maidenhair Tree, the free apex of the nucellus contained the pollen-chamber, a cavity serving for the reception of the pollen-grains (cf. Figs. 110, 111, p. 299). In *Lagenostoma*, however, the pollen-chamber is peculiar and more complex than in the recent Gymnosperms referred to; a solid column of tissue rises up in the middle of the cavity, leaving only a comparatively narrow,

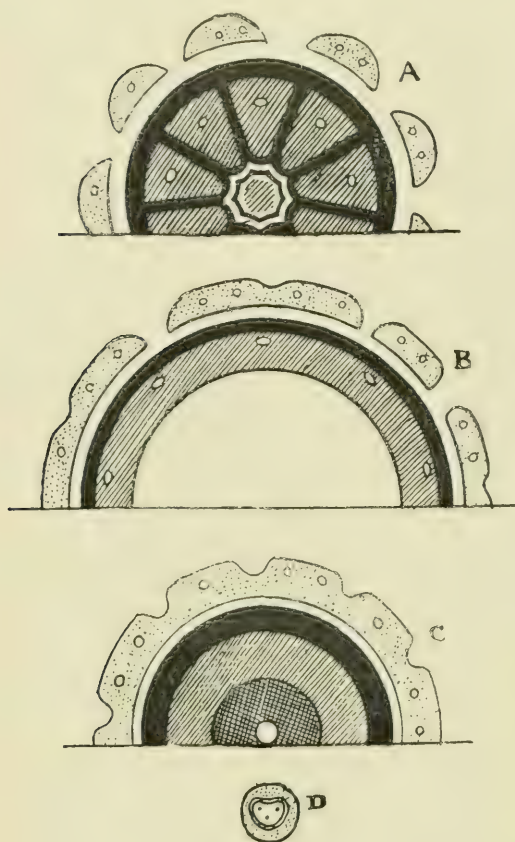


FIG. 35.—*Lagenostoma Lomaxi*. Diagrammatic transverse sections in the planes A, B, C, and D of Fig. 34. A (through micropyle) shows pollen-chamber, canopy of integument and free lobes of cupule; B (through body of seed) shows fused nucellus and integument, with vascular bundles, and cupule partly divided into lobes; C (through chalazal tissue) shows central bundle, chalazal tissue, base of integument, and continuous, furrowed cupule; D, section of the rachis-like pedicel. After Oliver.

annular space, available for the pollen-grains (see Figs. 33, 34, 35, A). The whole pollen-chamber or rather the apical part of the nucellus containing it, is flask-shaped, and was called, by Williamson, the *lagenostome* (flagon-mouth), a useful name, still employed for this particular type of

pollen-chamber. The neck projects a little through the micropyle, as an open tube, and no doubt received the pollen-grains directly, without their having first to traverse a micropylar passage (Figs. 33, 34). Pollen-grains are found in the lower part of the cavity of the pollen-chamber; it has been suggested that the annular form of the cavity was correlated with the arrangement of the archegonia. The pollen-grains themselves appear to have been multicellular, but this point is better shown in other plants (see Figs. 82, 83, 109, B, pp. 210, 211, 298).

In the interior of the seed the contour of the megaspore or embryo-sac can usually be traced (Fig. 33), but its membrane cannot always be distinguished from the disorganised tapetal layer of the nucellus. In an interesting specimen referred to *L. Lomaxi* and described by Prof. McLean,¹ a large part of the prothallus is excellently preserved, as shown, in approximately transverse section, in Fig. 36, A. It is retracted from the megaspore-membrane. The central part of the prothallus (obscure in the figure) consists of rounded cells; then comes a broad zone of large, radially elongated elements, and finally, at the periphery, there is a well-defined layer of small, squarish cells (see Fig. 36, lower drawing). The structure agrees closely with that of the prothallus of recent Gymnosperms, both Cycads and Conifers. The archegonia have not yet been observed.

The identification of the seed of *Lyginopteris oldhamia* afforded, for the first time, the proof that a member of the "Cycadofilices" was a seed-bearing plant, and led, as further evidence came in, to the establishment of the class Pteridospermeae.

The seed, as we have seen, is a remarkably complex one, already far enough removed from a cryptogamic megasporangium; there is indeed little trace of anything primitive about *Lagenostoma*, except perhaps the

¹ R. C. McLean, "Two Fossil Prothalli from the Lower Coal-measures," *New Phytologist*, vol. xi. 1912, p. 306.

fact that the reception of the pollen was a function of the nucellus—the sporangial part of the seed or ovule—and had not been assumed by the integument. This

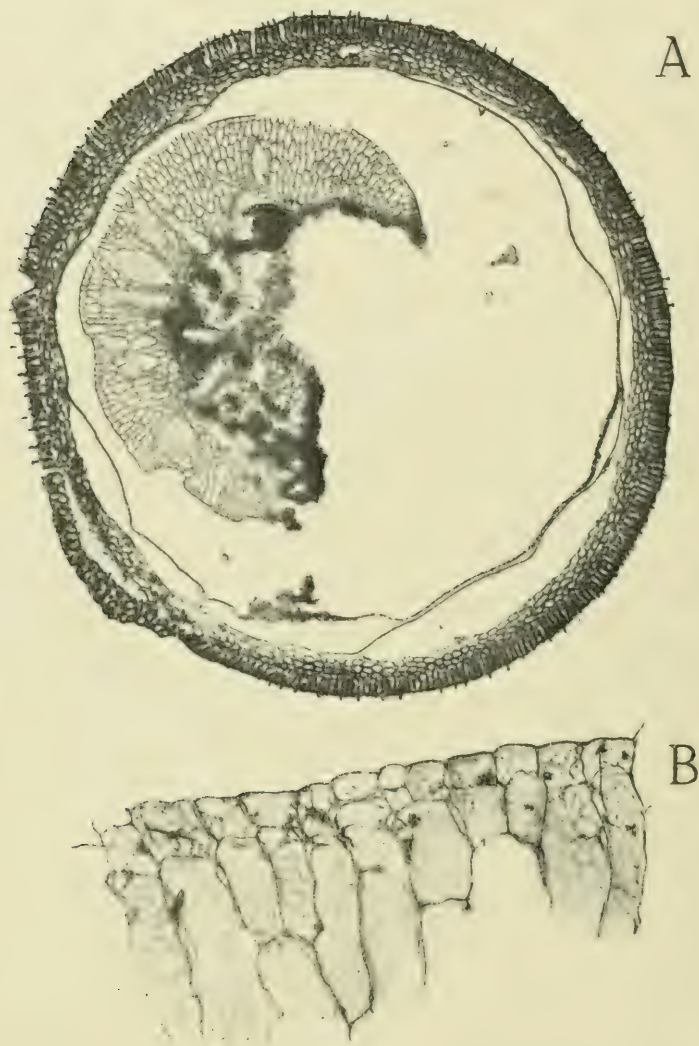


FIG. 36.—*Lagenostoma Lomaxi*. A, Transverse section of seed, showing the testa, remains of nucellus and megaspore-membrane, enclosing the prothallus, the greater part of which is preserved. \times about 18. B, outer tissues of prothallus, enlarged. After R. C. McLean, 1912. Reproduced from *The New Phytologist* by kind permission.

is an interesting peculiarity, but whether it was really primitive is quite an open question. So far as the seed itself is concerned, there is little to indicate any special affinity to the Ferns.

The absence of any trace of an embryo is a negative character common to all known Palaeozoic seeds, though there are many instances of the preservation of the archegonia (see, *e.g.*, Fig. 113, p. 307). Yet the seeds, as a rule, are evidently mature and not mere ovules. Neither, considering the frequent presence of pollen-grains in the pollen-chamber, can we assume that all the seeds found happened to be barren. It is possible that, though pollinated, they were not yet fertilised, the latter process perhaps taking place an appreciable time after the seeds were shed; or again, it may be that a resting stage followed immediately on fertilisation, before any marked development of the embryo had started. In any case it appears that the period of rest came much earlier with reference to the growth of the embryo than in most of our recent seeds. We find a relic of the old conditions in recent Cycads, in which the embryo is often scarcely to be recognised when the seed is ripe and ready for sowing. On the other hand the Mesozoic *Bennettites* was completely modern in this respect for there the embryo was far advanced, filling the whole embryo-sac, before the seed was shed (see Fig. 122, p. 334).

Returning to the seed of *Lyginopteris oldhamia*, we have seen that the structure of the pedicel and cupule shows that the seed-bearing organ formed part of a leaf. Evidence from allied species affords evidence that the seeds were borne on compound fronds or pinnae, only differing from the sterile foliage in the suppression of the laminae of the leaflets, or rather, perhaps, in their modification to form the cupules.

Other Species

Calymmatotheca Stangeri, a fructification of Lower Carboniferous age, described by Stur in 1877,¹ consists

¹ D. Stur, "Die Culmflora der Ostrauer und Waldenburger Schichten," *Abhand. der K. K. Reichsanstalt zu Wien*, Band viii. Heft ii.

of stellate, usually six-rayed bodies, borne, in the original specimens, on the naked rachis of a fertile frond. They are indicated in the restoration of *Lyginopteris* (Fig. 1, Frontispiece). A re-investigation of Stur's specimens confirmed his attribution of the fructification to a *Sphenopteris* closely similar to *S. Höninghausi* (the foliage of *Lyginopteris oldhamia*) and also his interpretation of the stellate bodies as foliaceous indusia, and not groups of sporangia, as others had conjectured. There is, in fact, little doubt that these organs are of the same nature



FIG. 37.—*Lagenostoma Sinclairi*. Portion of branched rachis, bearing cupulate seeds. Nat. size. After Arber.

as the cupules of *Lyginopteris oldhamia*, but, in Stur's specimens the seeds had been shed, perhaps prematurely. In a British specimen of *C. Stangeri*, from the Carboniferous Limestone Series of Yorkshire, kindly communicated to me by Dr. Kidston, there is a cupule in close association and possible connection with a frond of the

vegetative form of the species. This cupule is more closed than in Stur's examples, and may probably still contain the seed.

Dr. Newell Arber¹ described, under the name *Lagenostoma Sinclairi*, seeds preserved as carbonaceous impressions, of Lower Coal-measure age, which, in dimensions and external characters, agree generally with a *Lagenostoma* of the type of *L. Lomaxi*. As in that species each seed is invested by a lobed cupule (Figs. 37, 38). The cupulate seeds are borne on the terminations of the finer branches of a highly compound frond, with reduced lamina, in all probability of the *Sphenopteris* form. The crenatures at the tip of the ribbed seed suggest the

¹ E. A. N. Arber, "Some new Species of *Lagenostoma*, a Type of Pteridospermous Seed," *Proc. Royal Soc. B*, vol. lxxvi. 1905.

presence of a canopy. While the affinity of the seed with *Lagenostoma* is undisputed, the absence of internal structure has led to the employment of another generic name (*Radiospermum*, Arber; *Lagenospermum*, Nathorst) for seed-impressions of this nature. There is some probability, on grounds of association, that *Lagenostoma Sinclairi* may have belonged to the frond known as *Sphenopteris obtusiloba*, Brongn.

In *Sphenopteris Dubuissonis*, a Lower Coal-measure species from Brittany, allied to *S. Höninghausi*, Grand'Eury observed six-lobed cupules, in some cases still containing the seeds, borne on the ends of long, slender pedicels, identical with the ultimate ramifications of the rachis.¹

Other cases of cupulate seeds or cupules attached to a rachis have since been recorded by Dr. Kidston, the Abbé A. Carpentier and Dr. Marie C. Stopes.² All



FIG. 38.—*Lagenostoma Sinclairi*. Two seeds, enclosed in lobed cupules, and borne terminally on branches of the rachis. $\times 5$. After Arber.

¹ C. Grand'Eury, "Sur les graines de *Sphenopteris*, etc.," *Comptes rendus*, t. 141, p. 812, 1905.

² R. Kidston, "On the Fossil Flora of the Staffordshire Coal-Fields," Part iii. *Trans. Royal Soc. Edinburgh*, vol. 1. Part i. 1914, p. 160; A. Carpentier, "Fructifications et inflorescences du Westphalien du Nord de la France," *Rev. Gén. de Botanique*, t. xxiii. 1911; "Contribution à l'étude du carbonifère du nord de la France," *Mém. de la Soc. géolog. du Nord*, Lille, 1913, p. 390. M. C. Stopes, "The 'Fern Ledges,' Carboniferous Flora of St. John, New Brunswick," *Canada Dept. of Mines, Mem.* 41, 1914, p. 74.

the specimens are preserved in the form of impressions and in certain instances, as in Dr. Stopes's *Pterispermotrobis bifurcatus*, we are left in some doubt whether the fructification was a seed-bearing or pollen-bearing organ. The clearer examples, however, in which the seeds are evident, supplement in a satisfactory way the evidence of the structural specimens, and confirm the conclusion that the seeds of the *Lyginopteris* group were borne on the rachis of the frond. The analogy of the microsporangiate fructification, described below, establishes a certain presumption that the fertile rachis may have formed part of the same frond which elsewhere bore vegetative leaflets.

The well-known seed *Lagenostoma ovoides*, described by Williamson and recently investigated more fully by Miss Prankerd,¹ has the structure very perfectly preserved. No cupule has been detected with certainty, but the agreement with *L. Lomaxi* in all the important characters of the seed itself is so close as to leave no doubt that it belonged to some plant of the *Lyginopteris* type, and very possibly to a species embraced under the collective name of *L. oldhamia*. Other seeds, less closely allied, but of the same general affinity, will be mentioned below (pp. 80, 84).

The Microsporangia of Lyginopteris

Nothing definite was known of the male fructification of *Lyginopteris*, or indeed of any Pteridosperm, until Dr. Kidston in 1905 discovered a species of *Crossotheca* in organic connection with foliage, which he identified with that of *Sphenopteris Höninghausi*, and therefore with the frond of *Lyginopteris oldhamia*. The

¹ T. L. Prankerd, "On the Structure of the Palaeozoic Seed *Lagenostoma ovoides*, Will." *Linnean Society Journal—Botany*, vol. xl. 1912, p. 461.

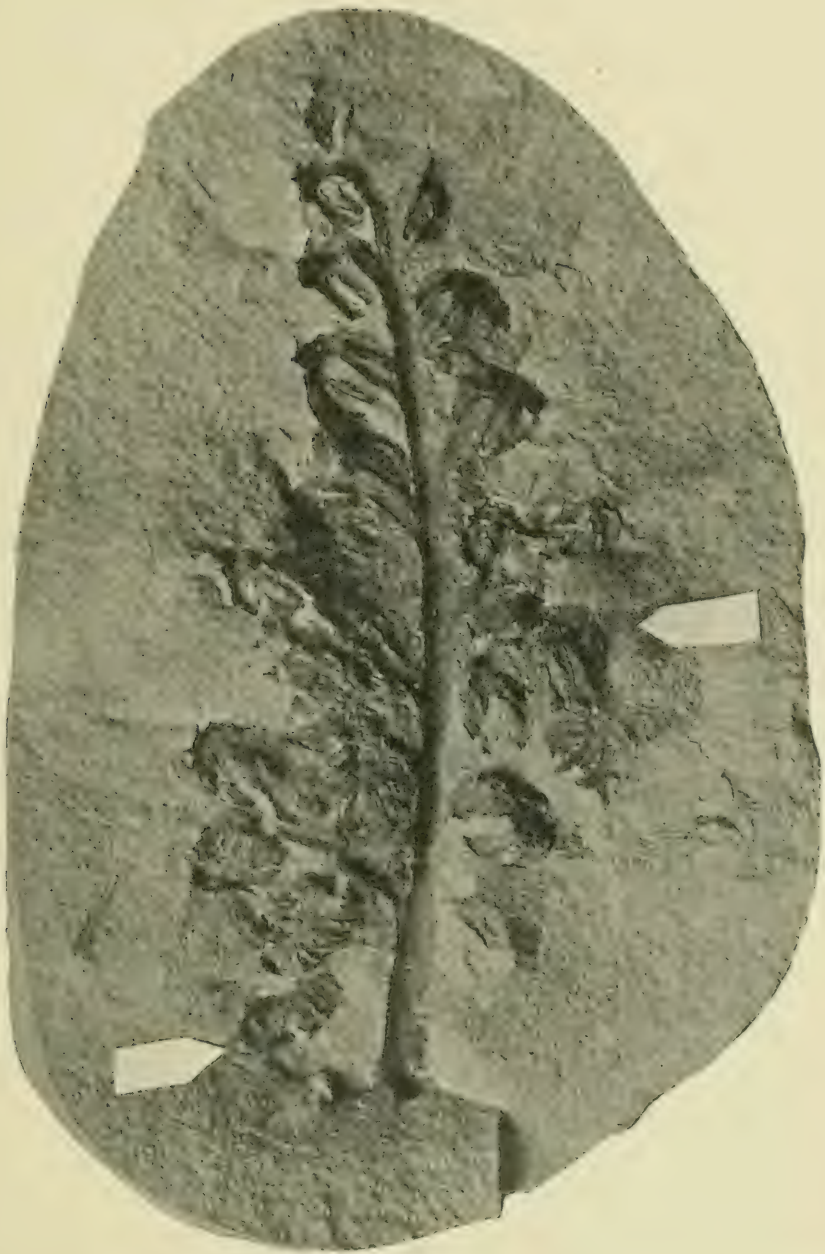


FIG. 39.—*Crossotheca Höninghausi* (the microsporangiate fructification of *Lyginopteris oldhamia*) Fertile pinna, contained in an ironstone nodule. On the ultimate branches of the rachis are borne the somewhat peltate fertile pinnules, from the under surface of which the long microsporangia hang down. $\times 3$. Enlarged from a photograph lent by Dr. R. Kidston, F.R.S.

name employed by Dr. Kidston is *Crossotheca Höninghausi*.¹

The genus *Crossotheca* was founded by Zeiller in 1883, on a fructification found by him in connection with a *Sphenopteris* ² (see Fig. 119, F, Vol. I. p. 255); the genus is characterised by the arrangement of the sporangia, hanging from the lower surface of the oval or spatulate fertile segment, the whole resembling an epaulet with its fringe. On account of the absence of an annulus and the appearance of a slight fusion between the sporangia, Zeiller referred *Crossotheca* to the Marattiaceae, a view generally adopted up to the date of Dr. Kidston's discovery. In the meantime a number of other species had been described, some with the Sphenopteroid and others with the Pecopteroid type of foliage.

Dr. Kidston's specimens were found in ironstone nodules from the Dudley Coal-field (Westphalian Series) (Fig. 39). The specimens are preserved in the form of casts, but in some cases the cavities are infiltrated with carbonate of lime and so retain their natural form and something of the original structure of the organs. Though most of the fertile specimens bear no sterile pinnules, in several instances the two forms occur in organic connection (see Fig. 40). Dr. Kidston has no doubt that the foliage is that of *Sphenopteris Höninghausi*, and therefore of *Lyginopteris oldhamia*.³

¹ R. Kidston, "On the Occurrence of Microsporangia in organic connection with the foliage of *Lyginodendron*," *Proc. Royal Soc. B*, vol. lxxvi. p. 358, 1905; "On the Microsporangia of the Pteridospermeac," *Phil. Trans. Royal Soc. B*, vol. 198, 1906.

² R. Zeiller, "Fructifications de fougères du terrain houiller," *Ann. Sci. Nat. (Bot.)*, ser. vi. t. xvi.

³ Dr. Kidston's identification was accepted by Zeiller and is generally admitted. Prof. Chodat in 1908 endeavoured to show that the true microsporangia of *Lyginopteris* are identical with the annulate sporangia described under the name of *Pteridotheca Williamsonii* (vol. i. p. 265). This, however, is a mistake; the leaflets on which the *Pteridotheca* sporangia are borne are quite different in structure from those of *Lyginopteris*. Dr. Gothan, in 1913, expressed doubt as to the specific identity of Dr. Kidston's specimens with *Sphenopteris*

The general structure and arrangement of the fertile pinnules are shown clearly in Fig. 39 from one of Dr. Kidston's photographs; the pinnules are oval in form, about 2 to 2.5 mm. in length, and borne on stout pedicels, the mode of insertion rendering them somewhat peltate. They are rather thick, and each appears to be traversed by a branched vein. "Each pinnule usually bore six, rarely seven, bilocular microsporangia. They are fusiform and end in a sharp point" (Kidston). When young, the sporangia were convergent, but they opened out later, assuming the fringe-like arrangement. A sporangium is about 3 mm. long and 1.5 mm. in maximum width, while each of the two loculi is about 0.5 mm. in diameter.

No evidence of cohesion among the sporangia was found; a bilocular sporangium may be interpreted as a synangium, and Dr. Kidston considers it probable that it has arisen through the coalescence of two sporangia (*l.c.* p. 430).

The nature of the preservation in the Dudley specimens is such as to leave the detailed morphology somewhat uncertain, but the occurrence of bilocular sporangia has since been observed in petrified material also (see Fig. 41). In *Crossothea Höninghausi* the microspores are still contained in the cavities of the



FIG. 40.—*Crossothea Höninghausi*. Fertile pinna in connection with sterile pinnæ of *Sphenopteris Höninghausi* (leaf of *Lyginodendron*). $\times 2$. R. S. From a sketch after a photograph lent by Dr. Kidston.

Höninghausi. See R. Chodat, "Les Ptéridopsides des temps paléozoïques, étude critique," *Archives des sci. phys. et nat.* t. xxvi. 1908, p. 22, Geneva; W. Gothan, "Die oberschlesische Steinkohlenflora, I. Teil, Farne und farnähnliche Gewächse," *Abhand. d. K. Preuss. Geol. Landesanstalt*, Neue Folge, Heft 75, 1913, p. 49.

sporangia. Each spore has a distinct triradiate ridge, indicating tetrahedral arrangement, and the surface of the outer wall is rough with minute points. The spores vary from 50μ to 70μ in diameter.

Dr. Kidston finds that "the cleft by which dehiscence took place passed longitudinally down the centre of the inner face of the microsporangium and thus the microspores of both loculi would be liberated simultaneously."

Another species of *Crossotheca*, named *C. Hughesiana* by Dr. Kidston, occurs in the Dudley nodules. The fertile pinnules are cordate in form and twice the size of those of *C. Höninghausi*, measuring about 5×5 mm. In all other respects, including the bilocular structure of the microsporangia, there is a close agreement with the former species. The sterile foliage of *C. Hughesiana* is unknown.

Shortly before Dr. Kidston's discovery of *Crossotheca Höninghausi*, Dr. Margaret Benson had described a fructification (*Telangium Scotti*) with structure preserved, from the coal-balls of Lancashire, and was inclined to attribute it to *Lyginopteris*.¹ The sporangia are long and pointed, somewhat resembling those of Dr. Kidston's *Crossotheca* in shape and size, but they are not bilocular, and are united in their lower part to form large synangia, often with as many as eight members.

Dr. Benson described the synangia as borne terminally on the ultimate ramifications of a rachis, without a limb, this being a distinctive character of her genus *Telangium*. As a matter of fact the synangia in *T. Scotti* are often seated on a flat disc or lamina, which may be compared to a fertile pinnule of *Crossotheca*, so that the distinction between the genera is not always as marked as it appears at first sight. At present the relation of *Telangium Scotti* to *Lyginopteris* or its allies is doubtful. An interesting point emphasised by Dr. Benson is the resemblance

¹ M. Benson, "Telangium Scotti," *Ann. of Bot.* vol. xviii. 1904. A preliminary note was published two years earlier.

between the spores of her *Telangium* and the pollen-grains found in the pollen-chamber of *Lagenostoma ovoides*.

Other species referred, more or less provisionally, to *Telangium* have been observed, both as impressions and petrifications; two of the former, of Lower Carboniferous age, *T. affine* and *T. bifidum*, are attached to the fronds of definite species of *Sphenopteris*, while an Upper Carboniferous species, *T. nutans*, Carpentier, is associated with *Sphenopteris obtusiloba*, which it resembles in the mode of branching of the rachis, the tufts of sporangia appearing to correspond in position to the tertiary pinnules of the sterile frond.¹



FIG. 41.—*Telangium*, *sp.* Transverse section of synangium, consisting of two coherent sporangia, each of which is divided into two loculi, by a partition, *p*. \times about 36. Univ. College Collection, R. 99. (G. T. G.)

As regards the petrified specimens of *Telangium*, which are frequent in the coal-balls of the Lower Coal-measures, there is no published information except in the case of *T. Scotti*, and the whole subject demands investigation. The specimen figured, by kind permission of Prof. Oliver, F.R.S., is provisionally referred to *Telangium*; its interest lies in the fact that it affords conclusive proof of the occurrence of bilocular sporangia, as found by Dr. Kidston in his less favourably preserved specimens of *Crossothecca*. The section figured (Fig. 41) is a transverse one of a bisporangiate synangium; the two sporangia clearly have a common wall where they

¹ See Carpentier's memoirs, cited on p. 73.

join. Each sporangium is divided into two loculi by a narrow septum at right angles to the common wall. The sporangial wall is several cells thick, the outer layer having conspicuous dark contents; the septa between the loculi are continuous at either end with sterile tissue in the interior of the sporangium; the loculi are filled with ill-preserved spores. There is no evidence at present as to the plant to which this fructification belonged. Other cases of bilocular sporangia have been observed in the petrified material. It is, however, remarkable that no petrified *Crossotheca*, as distinguished from a *Telangium*, has yet been identified in association with *Lyginopteris*, in the coal-balls.

Dr. Kidston's discovery that a *Crossotheca* was borne on a *Sphenopteris* of the same type as the frond of *Lyginopteris oldhamia* establishes a strong presumption that the *Crossothecas* generally, formerly regarded as Fern-fructifications, constitute the pollen-bearing organs of Pteridosperms. In bearing their microsporangia on modified pinnules of the ordinary frond, these plants show a lower degree of differentiation than any Spermatophytes previously known.

*Sphaerostoma, the probable seed of Heterangium
Grievii*

We have as yet no direct evidence as to the nature of the seed in any species of *Heterangium*. A seed, however, is frequently found in close association with the stem and foliage of *H. Grievii* in the Pettycur beds, and as there is no other plant present to which it is likely to have belonged, there is a fairly strong presumption that the two were connected. Attempts, however, to find actual continuity have proved unconvincing. *Sphaerostoma ovale*, as this Lower Carboniferous seed is now called, was originally described by Williamson under the names *Conostoma ovale* and

C. intermedium. The two species are now merged in one, and Dr. Margaret Benson, to whom we owe a full investigation of the Pettycur seed, has shown that it is generically distinct from *Conostoma* and has founded the genus *Sphaerostoma* to receive it.¹

Sphaerostoma ovale is a seed of the general type of *Lagenostoma*, a fact which agrees well with its attribution to *Heterangium*, an ally, as we have seen, of *Lyginopteris*. The seed is about 3.5 mm. in length, by 2.2 mm. in maximum diameter. Dr. Benson's restoration of the longitudinal section is reproduced in Fig. 42. In some of the specimens the seed is found enclosed in a cupule (Fig. 42, *c*), a somewhat delicate structure, traversed by vascular bundles (*v.b.*¹) and surmounting the micropyle. The presence of a cupule is an obvious point of agreement with the type represented by *Lagenostoma Lomaxi*. The cupule has been called an "outer integument"; it is, however, perfectly free from the seed within (Fig. 42).

The seed is radially symmetrical; the transverse section is circular in the middle region, becoming somewhat octagonal towards either end. The seed is built on the same lines as a *Lagenostoma*, the differences being in detail. The integument is fused with the nucellus, except at the upper end, in the region of the micropyle (Fig. 42, *i*). The epidermis of the free surface, whether external or within the micropyle, is papillate and was probably mucilaginous. The most conspicuous feature is the "frill" (Fig. 42, *f*), a crest of large, vertically elongated cells, surrounding the micropyle. Dr. Benson finds that the frill was not continuous, but was composed of about eight lobes with furrows between. Within the

¹ W. C. Williamson, "Organisation of Fossil Plants of Coal-measures," Part viii., *Phil. Trans. Royal Soc.* vol. 167, 1877, p. 244, Figs. 82-87. M. Benson, "*Sphaerostoma ovale* (*Conostoma ovale* et *intermedium*, Williamson), a Lower Carboniferous ovule from Pettycur, Fifeshire, Scotland," *Trans. Royal Soc. Edinburgh*, vol. 1. Part i. 1914.

epidermis is a mechanical zone of fibres, which at the chalazal end extends inwards, forming a sheath around the supply-bundle (*ch*). The latter enters the seed as a single strand, which branches repeatedly to form the

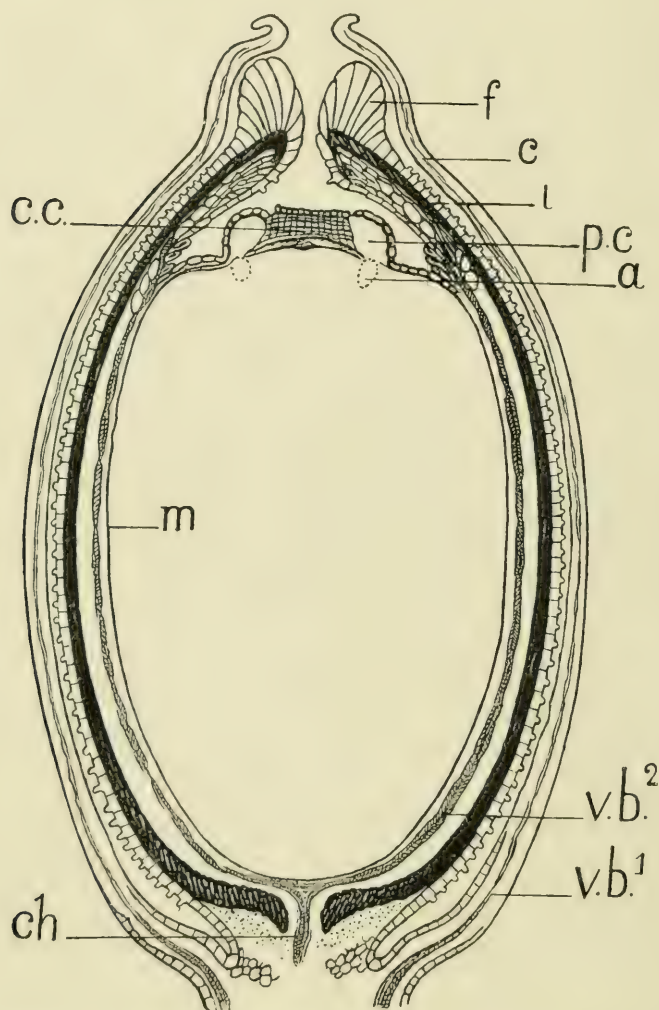


FIG. 42.—*Sphacrostoma ovale*. Diagrammatic, longitudinal section of seed, in its cupule. *c*, cupule; *i*, integument; *f*, frill of integument; *p.c.*, pollen-chamber; *c.c.*, central column; *a*, probable position of archegonia; *m*, megaspore-membrane; *v.b.¹*, vascular bundle of cupule; *v.b.²*, vascular bundle of integument; *ch*, chalazal strand. After Dr. Margaret Benson, F.L.S.

vascular system of the integument. In the body of the seed there are eight, or sometimes nine, bundles ranged in a ring (*v.b.²*). That the vascular system really belongs to the integument and not to the nucellus is indicated

by the fact that the bundles extend up into the canopy, far above the summit of the nucellus.

Little structure is preserved in the nucellus except at its free, upper end. Here the outer layer is perfect, forming the nearly horizontal plinth (to use Prof. Oliver's term) from which the dome of the pollen-chamber rises (Fig. 42, *p.c.*). The form and structure of the pollen-chamber or lagenostome present the chief distinctions from the genus *Lagenostoma*. The low squat dome, which contains the pollen-chamber of *Sphaerostoma*, does not even reach the micropylar passage, and is thus very different from the long tubular lagenostome of the other genus, which, as we have seen, extends through the micropyle to the exterior. A low central column is present in *Sphaerostoma*, and this again differs from the corresponding structure in *Lagenostoma*, not only in form but in the fact that the epidermis of the pollen-chamber wall stretches right over it (Fig. 42, *c.c.*). Thus the annular pollen-chamber appears to be closed, but there is evidence that circumscissile dehiscence took place, the wall splitting around the edge of the central column, as is indicated in the diagram. Dr. Benson supposes that there was a hygroscopic mechanism causing the wall to erect itself, thus opening the circular crevice, and then returning to its original position, effecting closure after the pollen-grains had been admitted. The epidermis forming the pollen-chamber wall has a different structure from that which covers the central column and also from that of the "plinth." The cells of the pollen-chamber wall are radially elongated and have their vertical membranes thickened, the whole thus bearing some resemblance to a multiseriate annulus. The rest of the epidermis is formed of ordinary isodiametric cells.

The megaspore membrane is preserved, sometimes accompanied by disorganised remains of nucellar tissue. Only doubtful traces of the prothallus have been detected.

The seed is evidently of the *Lagenostoma* type, and

there is every probability that it belonged to the closely associated *Heterangium Grievii*, though proof is still lacking. It may be pointed out that in the Lower Carboniferous *Sphaerostoma* pollination must have taken place in the ordinary Gymnospermous fashion, through the micropyle. This fact casts doubt on the primitive character of the peculiar mechanism of the later *Lagenostoma*, in which the pollen-chamber reached the exterior and appears to have received the microspores directly.

Other seeds, probably referable to Lyginopterideae

There are several seeds, of which the structure is well known, which appear to belong to the *Lagenostoma* group, and may therefore be referred with some probability to the Lyginopterideae. But at present there is no clue whatever to the particular plants which bore the seeds, so only a brief notice is called for here.

Perhaps the most remarkable of these isolated seeds is *Physostoma elegans* (*Lagenostoma physoides*), first described by Williamson in 1875 and 1877, and more recently investigated in detail by Prof. F. W. Oliver.¹

This is an Upper Carboniferous seed from the coal-balls of Lancashire and Yorkshire; an imperfectly preserved specimen from the Lower Carboniferous of Pettycur has been provisionally referred to the same genus by Dr. Gordon.

Physostoma elegans is a somewhat slender seed about 6 mm. in length by 2.25 mm. in maximum diameter. Its most remarkable feature is the structure of the micropylar region, for here the integument, instead of forming a continuous tube, is divided up into a circlet of about ten free tentacles (Fig. 43) surrounding and surmounting

¹ Williamson, "On the Organisation of the Fossil Plants of the Coal-measures," Part viii., *Phil. Trans. Royal Soc.* vol. 167, 1877, p. 241; F. W. Oliver, "On *Physostoma elegans*, Williamson, an archaic type of seed from the Palaeozoic Rocks," *Ann. of Bot.* vol. xxiii. 1909.

the apex of the nucellus. In the body of the seed, where the integument is continuous, the tentacles are represented by ribs (Fig. 43, B); each rib and tentacle is traversed by a delicate vascular bundle. The external surface of ribs and tentacles is clothed by a dense growth

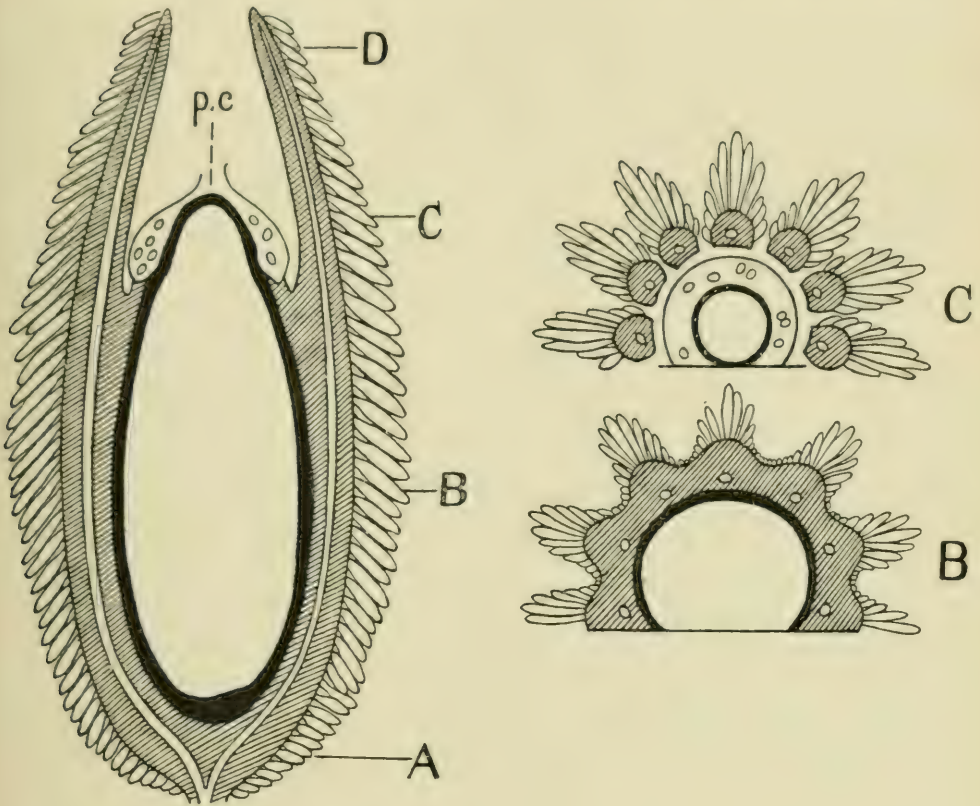


FIG. 43.—*Physostoma elegans*. Diagrammatic sections of seed. The longitudinal section shows the integument with the quill-like hairs, and the vascular bundles; the nucellus and megaspore. *p.c.*, pollen-chamber, containing pollen-grains. The transverse sections are taken at the levels B and C, B through the body of the seed, and C through the pollen-chamber. A, chalaza, D, micropylar region. After Prof. F. W. Oliver, F.R.S.

of large, overlapping, quill-like unicellular hairs, probably mucilaginous; the seed thus has a highly peculiar and characteristic appearance.

The nucellus is completely fused to the integument, except in the upper region; its tissues in the body of the seed are preserved and include a secretory layer and a tapetum next the embryo-sac. At the free end

is the pollen-chamber, which has an unusual form, owing to its floor being bulged in by the growth of the apex of the megaspore (Fig. 43). The most interesting feature of the pollen-chamber, however, is the great number of pollen-grains which it contains. In two successive sections of the same pollen-chamber nearly fifty pollen-grains were counted, so that the total number present must have been very considerable. Their abundance has raised questions as to the mode of pollination, whether anemophilous or entomophilous, questions which unfortunately cannot be answered. The pollen-grains have a multicellular structure, and in some cases had emitted bodies which have been interpreted as spermatozoids. The megaspore-membrane appears to have been thin; some remains of the prothallus have been observed.

The ring of free tentacles, replacing the micropylar tube, has been regarded as a primitive character; the chambers of the canopy in *Lagenostoma* may be considered as representing the tentacles in a fused and possibly more advanced condition. In any case, it is probable that the tentacles, though distinct, fitted closely together with the aid of their interlocking hairs, and thus formed an efficient corridor down which the microspores were guided to their goal.

While *Physostoma* is regarded as a relatively primitive type of seed, *Conostoma* as now understood seems to have been an advanced genus of the group. For the somewhat complicated structure reference must be made to the original descriptions. Our present detailed knowledge is due to the elaborate investigations of Oliver and Salisbury.¹ As shown by the adherent integument, the lagenostome and the canopy, *Conostoma* clearly belongs to the Lagenostomales, of which together with

¹ "On the Structure and the Affinities of the Palaeozoic Seeds of the *Conostoma* group," *Ann. of Bot.* vol. xxv. 1911. A valuable general account of this genus and of other Palaeozoic seeds will be found in Seward's *Fossil Plants*, vol. iii. 1917, chaps. xxix. to xxxi. and chap. xxxv.

Gnetopsis, to be mentioned immediately, it seems to represent the highest development. The cylindrical or slightly flattened seeds are ribbed or angular, the integument somewhat lobed at the apex. The vascular strands are equal to or fewer than the ribs or angles; the loculi of the canopy are nearly obliterated and equal the vascular bundles in number; the epidermis was mucilaginous.

The lagenostome is a minute, goblet-shaped organ, fitting exactly into the base of the highly developed micropyle. A cavity was formed in the plinth or upper part of the nucellus, and it is in this lower cavity and not in the lagenostome itself that the pollen-grains are found. Two species are described, *C. oblongum*, Williamson, from the English coal-balls, and *C. anglo-germanicum*, Oliver and Salisbury, which also occurs in the Westphalian and Rhenish petrifications of Langendreer and Duisburg.

In the second edition of this book the opinion was expressed that Renault's seed *Gnetopsis elliptica* was probably related to *Lagenostoma* and the Lyginopterideae. This view has now been fully confirmed by the investigations of Oliver and Salisbury. In the fructification described by Renault ¹ (referred by him to the Gnetaceae) four seeds (two of which are often abortive) are enclosed within a common envelope or cupule, consisting of two partly fused bracts, each of which is divided into about five teeth above and traversed by the same number of vascular bundles. The seeds or ovules are small (2.5 mm. long) and have a somewhat complex structure, which has been shown by Oliver and Salisbury to agree closely with that of *Conostoma*. The integument of *Gnetopsis* is traversed by four vascular strands as in *C. anglo-germanicum*, while the seed is slightly flattened as in *C. oblongum*. The lacunar region of the integument

¹ *Cours de bot. fossile*, t. iv. 1885, p. 179; Pl. xx. Pl. xxi. Figs. 1-6, Pl. xxii. Figs. 2-4.

near its apex, interpreted by Renault as a floating apparatus for transport by water, is shown by Oliver and Salisbury to correspond to the mucilaginous layer of *Conostoma*. On the other hand the apical plumes surrounding the micropyle, a conspicuous feature of Renault's genus, have not been found in *Conostoma*. Renault thought that they served first for guiding the pollen-grains to the micropyle and subsequently for effecting dissemination by the wind.

The lagenostome and plinth-chamber (the latter usually containing the pollen-grains) are essentially the same in both genera; the division of the lagenostome wall into lobes, observed in most specimens of *Gnetopsis*, is regarded by Oliver and Salisbury merely as an effect of maceration.

The common cupule, enclosing several seeds, is a striking feature which has so far only been observed in *Gnetopsis*. Nothing certain is known of a cupule in *Conostoma*. Oliver and Salisbury, however, point out that the hairs lining the cupule of *Gnetopsis* closely resemble those found, chiefly at an early stage, on the cupule of *Lagenostoma Lomaxi*. In *Gnetopsis elliptica* the prothallus, with indications of the archegonia, is preserved in several specimens.

Some other species referred to *Gnetopsis* have been described. One of them, *G. anglica*, Kidston, with the micropylar appendages more than 2 cm. long, is described from the middle Coal-measures of Barnsley, Yorks.

The genus is of great interest, especially from the light it throws on the nature of the cupule, which here, at any rate, cannot be interpreted as an outer integument. Renault called it an ovary.

AFFINITIES OF THE LYGINOPTERIDEAE

The anatomical characters of the family have already been briefly discussed (p. 60), with special reference to

the relation to Ferns. We found that this relation was to a great extent a matter of analogy; while the Lyginopterideae undoubtedly have more in common with the Ferns than with any other Cryptogamic phylum, there is no proof of genetic connection with any known group recognised as Ferns. In fact, the early Seed-plants, of which the Lyginopterideae are one family, may, for all we know, be as ancient as the Ferns themselves. The most we can assume is a common ancestry as yet unknown.

Now that we have considered such evidence as we possess regarding the reproductive methods of the family, we may take a more general view of its characters.

The seed clearly indicates affinity with Cycadophyta, though probably not a close one with the existing Cycadaceae. The adherent integument, its vascular system, and the pollen-chamber are all Cycadophytic characters.

While the definite attribution of the seed to a particular plant is still practically limited to the one case of *Lyginopteris oldhamia*, there can be no reasonable doubt that all the seeds grouped as Lagenostomales belonged to the same family of plants, *Sphaerostoma* probably being the seed of *Heterangium*. There is a considerable variety among the seeds in question, but it cannot be said that any of them are markedly primitive, or show much trace of the Cryptogamic megasporangium from which we assume that the seed was ultimately derived. In certain cases a remote analogy between the lagenostome-wall and a multiseriate annulus has been detected, but that is all. Any further consideration of the morphology of the seed may best be deferred till other types have been dealt with.

As regards the pollen-bearing organs our knowledge is still very limited. On the basis of Dr. Kidston's observations, we may be prepared to find that the Crossothecas generally were the male fructifications of the Lyginopterideae, though direct evidence is still confined

to a single case. As the bodies in question were formerly accepted as sporangial fructifications of Marattiaceae, their transference to Lyginopterideae has been regarded as indicating a certain affinity between the two families, and thus between Ferns and Pteridosperms. If indeed we might take the bilocular microsporangia of *Crossotheca Höninghausi* as typical, the structure would be very different from anything known in Marattiaceae or other Ferns. It is, however, probable that synangia such as those of *Telangium Scotti*, in which the sporangia are unilocular, may also have belonged to Lyginopterideae; and in that case an analogy with *Scolecopteris* would be evident; at present, however, our knowledge is too imperfect to justify further speculation.

Where the foliage of the Lyginopterideae is known, it is of the Sphenopteris form. If, however, we may take the *Crossotheca* type of microsporangiate organ as characteristic, the family was not limited to Sphenopteroid foliage, for various species of *Crossotheca* are known to have been borne on Pecopteroid fronds. Three such species are enumerated by Dr. Kidston,¹ besides two other Pecopterids which Prof. Zeiller regarded as probably belonging to *Crossotheca*. One of the latter, *Pecopteris exigua*, is of special interest, as the structure of the synangia is known and bears a considerable resemblance to that of *Telangium Scotti*.²

Anatomically, *Lyginopteris*, as is well known, shows a certain relation to the Cycads. The primary bundles are isolated from one another and are disposed round a large pith. The whole organisation of the vascular zone, both primary and secondary, is, broadly speaking, what that of a Cycad would be if the mesarch structure of the foliar bundles were continued downwards from the petiole into the stem (see above, p. 27, Figs. 14 and 15). We now know that this actually occurs in

¹ "The Microsporangia of the Pteridospermeae," *l.c.* p. 432.

² B. Renault, *Cours de bot. fossile*, t. iii. Pl. xix. Figs. 13-18.

certain Cycadean peduncles, which are themselves portions of the stem. The validity of a comparison between the mesarch xylem of a *Lyginopteris* and that of a Cycad has, however, been disputed by Prof. Chodat; he points out, quite correctly, that in the Cycadean foliar bundle the protoxylem is in connection with the centripetal xylem, while in *Lyginopteris* (and the same applies to *Heterangium*) it abuts on the centrifugal portion. This involves a different order of development of the metaxylem elements in the two cases. In Cycads the first development is inwards from the protoxylem, to form the centripetal wood; the centrifugal portion being added later. In *Lyginopteris*, on the contrary, it may be assumed that differentiation, starting from the protoxylem, first extended to the centrifugal metaxylem, subsequently spreading round on both sides, to form the centripetal portion. This is confirmed by the fact that spiral and scalariform tracheides form the centrifugal xylem (*i.e.* its primary part), while those of the centripetal wood present the definitive pitted structure. Prof. Chodat therefore regards the *Lyginopteris* bundle as forming a "closed divergent" (Bertrand and Cornaille) of a purely Filicinean type, as in *Osmunda*, and as quite unrelated to the mesarch bundle of the Cycadean leaf.¹

There is no doubt that Chodat has called attention to what, on the whole, is a real distinction. It is not, however, quite constant. Thus in the mesarch bundles occurring in the peduncle of some Cycads the protoxylem is usually connected with the centrifugal part of the wood; in some foliar strands it is in contact with both parts.² Mr. A. S. Marsh found that near the base of the petiole in *Stangeria* there is some primary centrifugal xylem in contact with the protoxylem, and internal to

¹ R. Chodat, "Les Ptéridopsides des temps paléozoïques," *Archives des sci. phys. et nat.*, Geneva, t. xxvi. 1908, pp. 10-20.

² Scott, "Anatomical characters presented by the Peduncle of Cycadaceae," *Ann. of Bot.* vol. xi. 1897, p. 399.

the secondary portion.¹ For the most part, however, and sometimes wholly, the centrifugal xylem of the Cycadean bundle is no doubt secondary, as Dr. Le Goc has rightly pointed out,² criticising a former view of my own. It is probably on this fact that the distinction emphasised by Prof. Chodat depends. Wherever secondary growth takes place, there is always a tendency for any primary centrifugal wood to become merged in the secondary. The first-formed elements will then necessarily belong to the only primary portion which remains—the centripetal xylem.

In *Poroxylon*, with a stem-structure much like that of *Lyginopteris*, the xylem-strands have become exarch, the protoxylem thus being in connection with the centripetal wood, while all the centrifugal part is secondary.³ This case seems to be quite parallel to that of the foliar bundles of Cycads.

Prof. Chodat's distinction is an interesting one, but a transition from one type to the other can quite well be traced. Taking the seeds into consideration, it seems that a certain affinity between *Lyginopterideae* and Cycads must be admitted, though it is improbable that the two groups have any direct genetic relation.

Our knowledge of the *Lyginopterideae* is still too fragmentary for it to be possible to draw up the essential characters of the family. The following points may, however, be mentioned, as likely to occur in plants of this relationship:

Leaves filicoid (Sphenopteroid or Pecopteroid).

Stem monostelic; leaf-trace single or double, sometimes undergoing further divisions; vascular bundles collateral in stem, becoming concentric in leaf-trace. Xylem mesarch.

¹ A. S. Marsh, "Notes on the anatomy of *Stangeria paradoxa*," *New Phytologist*, vol. xiii. 1914, p. 18.

² M. J. Le Goc, "Observations on the centripetal and centrifugal xylems in the petiole of Cycads," *Ann. of Bot.* vol. xxviii. 1914, p. 183.

³ See p. 247, Fig. 90.

Reproductive organs borne on somewhat modified pinnæ of the frond.

Microsporangiate organs of the *Crossotheca* or *Telangium* type. Seeds with radial symmetry, of Cycadean type, enclosed in a cupule. Integument adherent to nucellus, with a single vascular system. Pollen-chamber (lagenostome) present.

The relations of the Lyginopterideae to other groups will be further discussed at a later stage.

CHAPTER II

PTERIDOSPERMEAE—*continued*

Rhetinangieae ; *Megaloxyleae* ; *Calamopityeae* ;
Stenomyeleae ; *Protopityeae* ; *Cladoxyleae*

WE now go on to consider a series of families, some of which show a decided affinity with Lyginopterideae, while others are of altogether doubtful position. In none of them is there, as yet, any evidence as to the fructification ; they are included under Pteridosperms solely on the ground of anatomical characters. In the following chapter we shall return to groups that are known to have borne seeds, and are therefore *Pteridosperms*, in the strict sense.

In the last edition of this book, Potonié's name "Cycadofilices" was retained for families only known anatomically, while the newer name Pteridosperms was restricted to those groups in which there was some evidence, however partial, for reproduction by seeds. The distinction, however, is in no way a natural one, being based merely on our ignorance, and has proved impossible to carry out in practice. It has therefore been decided to employ the name Pteridospermeae in the widest sense, to embrace the whole plexus of Palaeozoic plants which show in their structure an analogy with Ferns on the one hand, and an approach to Gymnosperms on the other. Within this plexus we know that the seed-habit existed in members of two families (the

Lyginopterideae and the Medulloseae),¹ widely diverse in anatomical respects, as well as in other groups of which the anatomy is unknown. There is thus evidence that reproduction by seeds was widespread among Fern-like plants of Palaeozoic age, and there is a certain presumption, though of very unequal strength, that it may have extended to all the families in question. These considerations may justify the provisional use of the class-name Pteridospermeae² for the whole series.

The families described in the present chapter follow most naturally on the Lyginopterideae. We begin with a type which has much in common with *Heterangium*.

RHETINANGIEAE

Rhetinangium, Gordon

The only species, *R. Arberi*, was discovered by Dr. W. T. Gordon in the Pettycur Beds of the Calciforous Sandstone Series. It is thus of Lower Carboniferous age, the contemporary and associate of *Heterangium Grievii*. The two excellently preserved specimens have been fully described by the discoverer.³

One of the fragments was as much as 10 inches long: the stem was presumably a tall one, perhaps of scrambling habit, as Dr. Gordon suggests.

In its more obvious anatomical features the stem is like that of a large *Heterangium* (Fig. 44) and the size is about the same, the diameter being approximately 2 cm. The central cylinder is a protostele, the primary

¹ See Chapter III.

² The name Cycadofilices is also still employed as a synonym for Pteridospermeae, as for example by Dr. Lotsy, in his well-known *Botanische Stammesgeschichte*. This use of the name is quite unobjectionable, except, perhaps, on the ground that not all Pteridosperms show an affinity to Cycads.

³ Gordon, "On *Rhetinangium Arberi*, a new Genus of Cycadofilices from the Calciforous Sandstone Series," *Trans. Royal Soc. Edinburgh*, vol. xlviii. Part iv. 1912.

wood forming a solid mass, consisting of groups of tracheides in a network of cellular tissue, as in *Heterangium* (Fig. 45). This is surrounded by a zone of secondary wood and bast. The cortex has a strong mechanical construction, with radially arranged fibrous bands of

great depth. Perhaps the most striking feature, if the section happens to pass through a node, is the enormous size of the leaf-base, almost equalling that of the whole stem (Fig. 44). The arrangement of the leaves was spiral, but the phyllotaxis has not been determined.

So far, however, no fundamental difference from the *Heterangium* type of structure strikes the eye. The individual packets of tracheides are, it is true, somewhat larger in *Rhetinangium*, and the intervening tracts of cellular tissue somewhat broader, but these are trifling distinctions. The tracheides



FIG. 44.—*Rhetinangium Arberi*. Transverse section of stem and petiole-base. The stem is above: the enlarged petiole-base below. $\times 23$. From W. T. Gordon.

are just like those of Lyginopterideae, for they are long elements with numerous rows of bordered pits on their walls. The xylem-parenchyma and other cellular tissues of the stem contain numbers of elongated secretory sacs with dark contents and also shorter cells of a similar nature, but such differentiated elements are frequent in some species of *Heterangium*.

It is when we come to examine the outer border of the primary wood that the first great difference from *Heterangium* reveals itself. In *Rhetinangium* the peripheral strands of xylem are not mesarch but exarch, the small elements of the protoxylem lying on the extreme outside of each strand, adjacent to the secondary wood. Longitudinal sections show that the smallest tracheides are spiral.

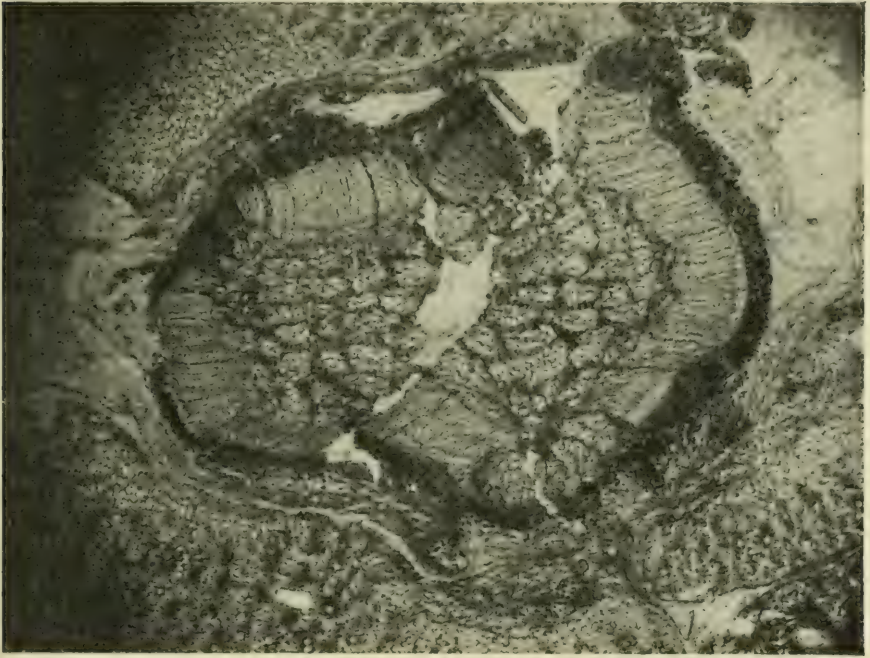


FIG. 45.—*Rhetinangium Arberi*. Transverse section of stele and adjacent tissues, showing primary and secondary wood, and inner and outer cortex. At three points leaf-traces are passing out from the stele. $\times 8$. From W. T. Gordon.

The pericycle, not always so sharply defined as in *Heterangium*,¹ is a delicate tissue, in which the "secretory sacs" are especially abundant. The cortex, in its inner part, consists of a uniform tissue of short, rather thick-walled cells: the sclerotic plates, so characteristic of *Heterangium*, are absent. The outer cortex, with its

¹ Dr. Gordon does not distinguish between pericycle and inner cortex. From the analogy of the Lyginopterideae it seems preferable to regard the whole thin-walled zone of tissue as pericycle.

beautiful mechanical system of strong, fibrous bands of great radial depth, far exceeds in its development anything that we find in *Heterangium* and is even more elaborate than in *Lyginopteris*; it rather recalls the corresponding region in the stem and leaf-stalk of the *Medulloseae*, to be described in Chapter III. The fibrous strands, viewed tangentially, unite with one another at long intervals, forming a narrow-meshed network: they are accompanied by long secretory sacs, and the tissue between them is often dilated.

We have next to consider the leaf-trace and petiole. The leaf-trace is the most characteristic feature of the genus, and appears to be unlike that of any other plant known. Three traces, at different stages of emission, are usually seen in the transverse section (Fig. 45). The trace, from its first differentiation, includes several of the peripheral xylem-strands of the stele, and increases in complexity as it passes outwards. An example is shown in Fig. 46, where it is just separating from the wood. The trace consists, as regards its xylem, of a number of tracheal strands united by xylem-parenchyma, and irregularly fusing on the inner side to form U-shaped masses. The whole thus has a complex, corrugated form, as seen in transverse section. The protoxylem-groups are numerous (as many as nine or ten in some cases) and are placed at the extreme outer edge of the xylem-strands constituting the massive trace (Fig. 46). Thus the structure of the leaf-trace, like that of the stelar xylem, is exarch. It has no secondary tissues of its own.

The complex trace never breaks up into separate bundles; it passes out, with little change, into the leaf-base and petiole, and retains its corrugated form even in the branches of the rachis. It is thus equally different from the single leaf-trace of the sub-genus *Eu-heterangium* and from the completely divided trace of the *Polyangium* species of *Heterangium*. It is essentially on account

of the exarch xylem and the complex, but not multiple leaf-trace, that *Rhetinangium* is placed in a distinct family from the Lyginopterideae. Owing to the imperfect preservation of the phloem, it is difficult to decide whether the trace was concentric or collateral. The appearances point to its having been concentric after entering the leaf-base, but we do not know at what point this structure was acquired.

Where the leaf-trace enters the cortex from the stele, the incipient leaf-base is marked off on either side

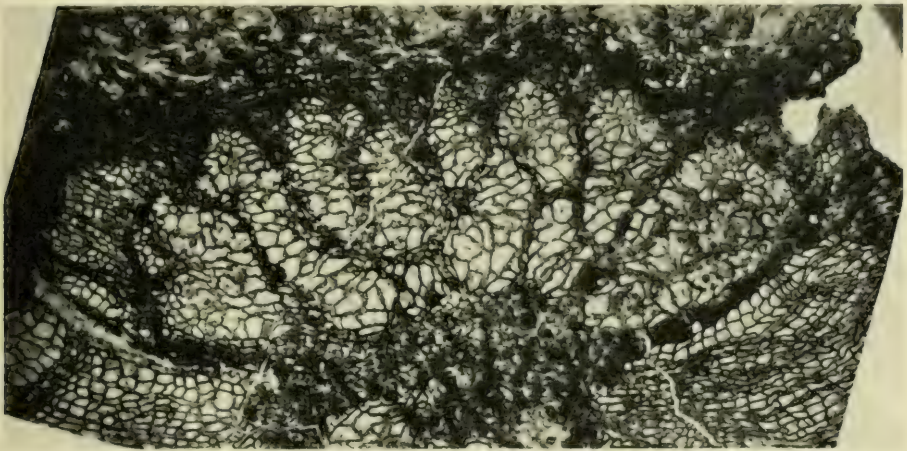


FIG. 46.—*Rhetinangium Arberi*. Transverse section of leaf-trace departing from stele; the secondary wood of stele is seen on either side; the compound leaf-trace has numerous external protoxylem-groups. $\times 30$. From W. T. Gordon.

by an extension of the fibrous bands inwards, across the inner cortical zone. A little higher up, as already mentioned, the leaf-base becomes enormously swollen, at the same time changing its structure. At a certain level all the fibrous bands disappear, and the whole leaf-base is merely a uniform mass of cellular tissue, with the vascular bundle at its inner edge (Fig. 44). We may conjecture from the analogy of recent leaves that the leaf-base was of the nature of a pulvinus, adapted perhaps to execute day and night or other movements, with which the presence of rigid mechanical tissues would have interfered.

Higher up the petiole the ordinary structure is assumed; the fibrous bands reappear, beginning on the adaxial surface; on the opposite side they first show themselves in a deep-seated position, only resuming a more external station at a higher level. Finally, the free petiole acquires the same mechanical construction as the stem, the diameter of the whole diminishes, and the vascular bundle takes up a central position. The leaf was, no doubt, a compound one, but no details of its form are known.

Returning to the stem, the zone of secondary wood and phloem is quite like that of a *Heterangium*. The principal rays correspond to the cellular bands between the primary xylem-strands, though the distinction between principal and secondary rays is not always conspicuous (Fig. 45). The rays, where they pass through the phloem-zone, are often dilated.

In one or two cases, the bases of adventitious roots have been observed on the stem, inserted either on the leaf-trace or near its point of emission. They appear to be tetrarch and possess secondary tissues. Nothing certain is known as to the free roots.

Dr. Gordon considers that the affinities of *Rhetinangium* are closest with the genus *Megaloxylon*, Seward, which will be described in the next section. The chief points in common are the exarch xylem and the large leaf-trace with several abaxial protoxylem-groups. Somewhat similar grounds of comparison may be found with *Sutcliffia*, one of the Medulloseae. These relations will be best discussed when we have described the genera in question. Both *Megaloxylon* and *Sutcliffia* are Upper Carboniferous plants, much later geologically than *Rhetinangium*.

In the meantime something more must be said as to the relation of *Rhetinangium* to the Lyginopterideae and especially to *Heterangium*, the only comparable genus of equal antiquity. In anatomical habit there is

undoubtedly a great similarity between the two genera. The points of agreement have been sufficiently dwelt on in the course of the description. Broadly speaking, the general harmony in anatomical plan seems sufficient to indicate a certain degree of real affinity. After all, *Rhetinangium* is more like *Heterangium* than anything else.

The important distinctions lie in the exarchy of the xylem and the complexity of the leaf-trace. In *Heterangium* the degree of mesarchy varies, as we have seen, in the different species, but the exarch condition is never reached. Its complete attainment would involve, it would seem, a somewhat important change, for the centrifugal portion of the xylem, small as it may be, appears to have been the part first formed, as shown by its immediate contact with the protoxylem and by the character of its tracheides. Its disappearance would therefore involve a change in the direction of the first differentiation of the xylem (see above, p. 91).

The other important distinctive character of *Rhetinangium*—the complex leaf-trace—is quite different from anything met with in Lyginopterideae, where the leaf-trace, as it starts from the stele, always consists either of one simple strand or of two such strands, separate from one another. Dr. Gordon points out how the union of a number of *Heterangium* leaf-traces, with the loss of their centrifugal xylem, might give rise to the *Rhetinangium* type of trace, but, as he realises, no transition between the two conditions is actually known.

In the present state of our knowledge we have no other course open to us but to leave *Rhetinangium* in a family by itself.

MEGALOXYLEAE

Megaloxylon, Seward

Here again we have to do with a monotypic family, containing a single genus with a single species, *Megalo-*

xylon Scotti, Seward. In this case our knowledge is further limited to one incomplete specimen, of which the wood only is known. The scanty material available has, however, been so thoroughly worked out by Prof. Seward¹ as to put us in possession of data of considerable interest and importance. The fragment, previously undescribed, was found in the Binney Collection at Cambridge: it came from the Lower Coal-measures of Lancashire, and is thus of Upper Carboniferous age. The association of the specimen with Goniatite shells shows that it was derived from a roof nodule: the Flora of such nodules, probably representing drifted remains, is often different from that of the ordinary coal-balls occurring in the underlying seams of coal.

The specimen was part of a rather large stem, measuring, in its incomplete condition, about 4.5 cm. in diameter. The central axis of primary wood reaches a diameter of 1.9 cm., the remainder of the fragment consisting of a zone of secondary wood (Fig. 47, A and B).

The primary structure is that of a protostele, for the wood extends to the centre, but it is a protostele of a very peculiar kind. The primary wood is made up of intermingled tracheides and cellular tissue; the tracheides throughout the greater part of the cylinder and the whole of its central region are of large diameter, but extremely short, the breadth commonly exceeding the length (Fig. 48, B). Their walls bear numerous bordered pits. In some places the short elements extend as far as the inner edge of the secondary wood, but this is only the case in the intervals between the leaf-traces, which have a different structure (Fig. 48, B). The short, wide tracheides are often arranged in transverse bands, the parenchyma between the bands having contracted so as to give rise to horizontal gaps recalling the discoid pith

¹ A. C. Seward, "Notes on the Binney Collection of Coal-measure Plants, Part ii. *Megaloxylon* Gen. nov.," *Proc. Cambridge Phil. Soc.* vol. x. Part iii. p. 158, 1899.

of Cordaiteae (see p. 270). As Prof. Seward suggested, the dilated tracheides of the primary xylem probably served for the storage of water.

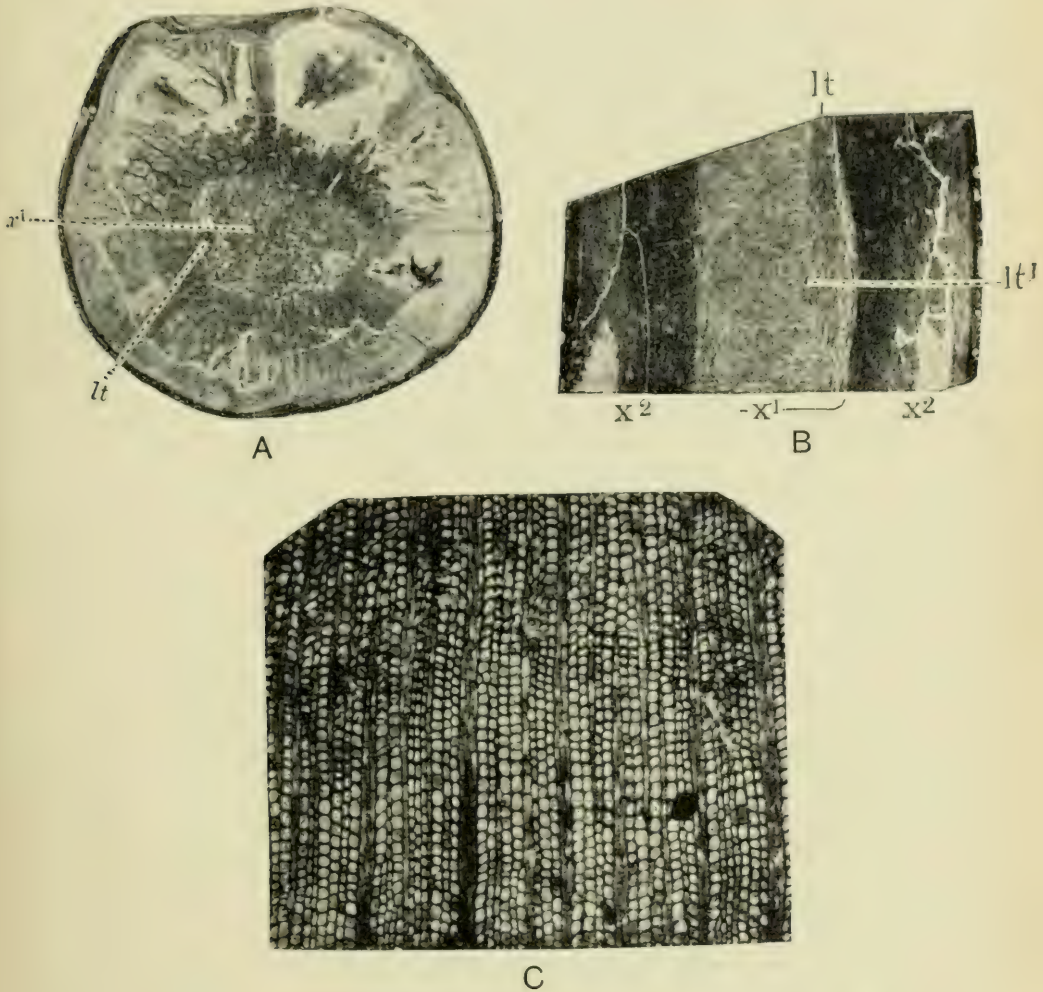


FIG. 47.—*Megaloxylon Scotti*. A, Transverse section of stem (wood only). x^1 , primary wood, surrounded by a broad secondary zone; lt , leaf-trace. Natural size. B, Radial section of the same. x^1 , primary, x^2 , secondary wood; lt , leaf-trace, still compact; lt^1 , the same trace lower down, becoming merged in the metaxylem. Natural size. C, Transverse section of secondary wood. $\times 24$. From Seward's *Fossil Plants* (Cambridge Press), by kind permission of the author and publishers and of the Cambridge Philosophical Society.

The large leaf-traces lie in the peripheral part of the primary cylinder; they are five in number in the transverse section and are cut at different levels, the arrangement implying a $\frac{2}{5}$ phyllotaxis. The comparison of

transverse and longitudinal sections has revealed the changes which the leaf-trace undergoes as it passes down the stele. When it first enters the primary cylinder the trace forms a fairly compact, oval mass, as seen in transverse section, consisting, as the longitudinal section shows, of long, normal tracheides of moderate diameter, interspersed with cellular tissue (Figs. 47, B and 48, B). The protoxylem lies on the extreme outside of the strand, next the secondary wood, and forms several groups, usually about six (Fig. 48, A). Thus the structure is completely exarch. Followed downwards, the trace gradually spreads out, the proportion of parenchyma to tracheides increasing; at the same time the inner tracheides of the trace become wider and shorter and gradually become merged in the general metaxylem¹ of the cylinder. As the trace expands, the protoxylem-groups on its outer margin become more widely spaced. The outer part, adjacent to the protoxylem, is the last to be affected by the change, but step by step the whole trace loses itself in the general primary wood, and ultimately the protoxylem itself dies out.

It is only the leaf-traces that possess protoxylem-elements; in the transverse section there are five traces and about thirty protoxylem-groups altogether—six to each trace. In the intervals, where the metaxylem abuts directly on the secondary wood, no protoxylem exists. The fan-like downward expansion of the leaf-trace and its gradual merging in the metaxylem appear to be peculiar to *Megaloxylon*.

The secondary wood has a somewhat compact structure (Fig. 47, C); it consists of pitted tracheides of the usual multiseriate type, with rather high medullary rays from one to five cells in width. The wood presents no peculiarities, but it is interesting to find that the large leaf-trace, where it passes out through the secondary zone, is sur-

¹ The word "metaxylem" is here employed, somewhat loosely, for all the primary wood apart from the leaf-traces.

rounded by a secondary ring of xylem of its own. No division of the trace has been observed, but we must

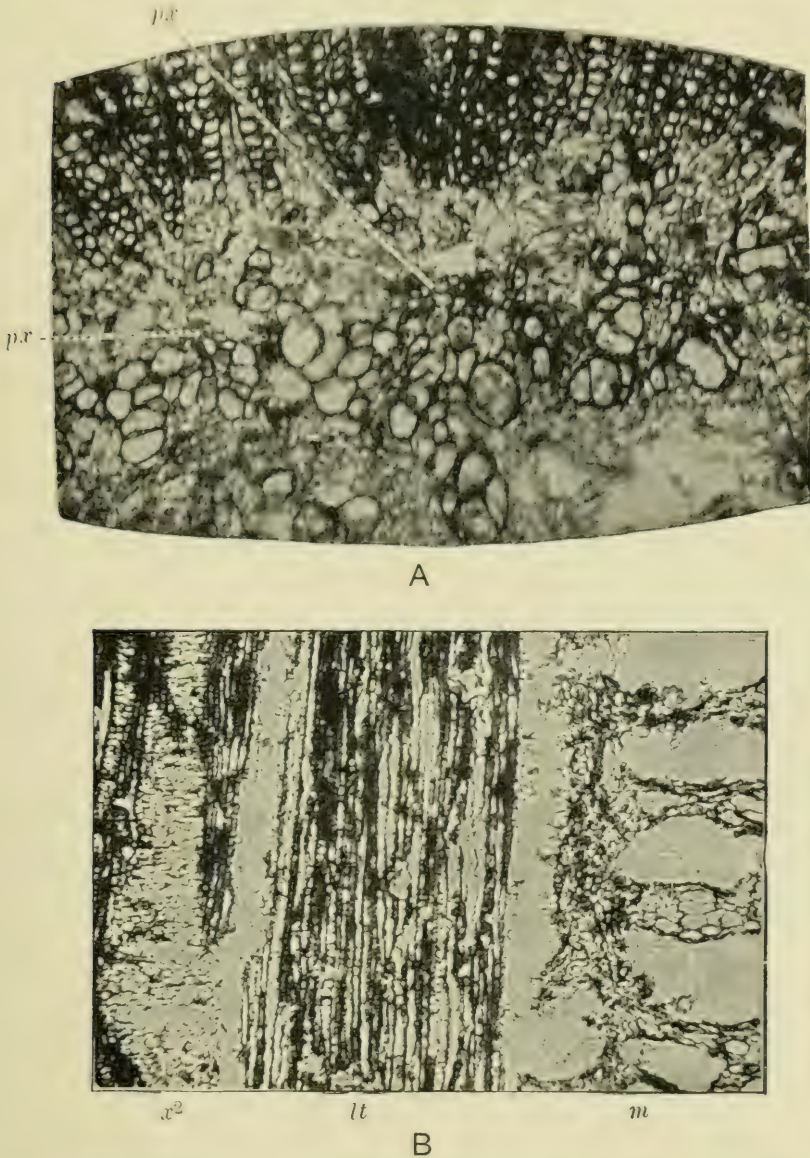


FIG. 48.—*Megaloxylon Scotti*. A, Transverse section at the junction of the primary and secondary wood (the latter above). *px, px*, protoxylem groups of the primary wood. $\times 50$. B, Radial section from the same region. *x²*, secondary wood; *lt.*, large leaf-trace; *m*, metaxylem, showing discoid structure. $\times 16$. From Seward's *Fossil Plants* (Cambridge Press), by kind permission of the author and publishers and of the Cambridge Philosophical Society.

remember that nothing is known of its course beyond the limits of the secondary wood.

In considering the relationships of *Megaloxylo*n, the first point to note is that the plant must have been monostelic, for leaf-traces are given off on all sides of the vascular cylinder alike. If the specimen had represented a single stele of a polystelic stem, such as that of the Medulloseae (see p. 175), the traces would have been limited to one side.

The protostelic organisation and the character of the pitting on the tracheides indicate that the genus must be placed among the simpler Pteridosperms or Cycadofilices. Among these, the nearest resemblance is to *Rhetinangium*, as was pointed out by Dr. Gordon. The two genera agree in the exarch xylem and the large leaf-traces with numerous protoxylem-groups. In other respects, however, they are very different. There seems to be no analogy in *Rhetinangium* (or indeed elsewhere) for the downward spreading-out and ultimate " nirvana " of the leaf-trace of *Megaloxylo*n.

The sectional form of the trace is quite unlike, the trace of *Megaloxylo*n being a strand of simple compact form, while that of *Rhetinangium* is corrugated and evidently compound. Another point of difference is in the distribution of the protoxylem-groups, which are strictly limited to the leaf-traces in *Megaloxylo*n, while in *Rhetinangium* they appear to extend all round the primary cylinder.

The peculiar structure of the metaxylem in *Megaloxylo*n is of course quite different from anything in *Rhetinangium*, though analogies are not wanting in other genera. For example, in *Zalesskya* and *Thamnopteris* among the Permian Osmundaceae, in *Diplolabis* among the Zygopterideae, and in *Lepidodendron selaginoides* the differentiation of the central xylem in the form of short tracheides is characteristic. This is an adaptive change, which seems to have occurred in various distinct phyla, where the central xylem had presumably become superfluous for conducting purposes, and found a use as an

organ for water storage.¹ A more remote analogy is found in a plant which we include in another family of Pteridosperms, *Calamopitys fascicularis*, where the inner secondary tracheides have undergone a similar modification. Some further newly discovered cases will be mentioned below (see *Bilignea*, p. 134).

It may be that *Megaloxylon*, so much later in geological age than *Rhetinangium*, represents an advanced scion of the same stock, but this is a pure conjecture. At present the genus remains isolated, like so many of the plants grouped under the vague but useful name of Pteridosperms.

CALAMOPITYEAE

It is an interesting fact that this family and the three which follow, as well as the *Rhetinangieae*, already described, are all of Lower Carboniferous age, while some of their members may even go back to the Upper Devonian. *Heterangium*, too, among the *Lyginopterideae*, belongs in part to the Lower Carboniferous flora. It is evident that at a comparatively early geological period a considerable number of distinct types of Pteridosperms already existed; at the same time most of these forms are so isolated as to show that our knowledge is still extremely fragmentary, and that only a few chance examples of what must then have been a great and varied class of plants have come down to us. Unfortunately, with the exception of *Heterangium Grievii*, we have no evidence as to the fructification in any of these Lower Carboniferous types. But on the anatomical data it seems clear that this distinct phylum, uniting, to a certain extent, fern-like characters with those of Gymnosperms, is among the oldest groups of the Vasculares.

The family *Calamopityeae* is better represented than the two last considered, for five species have been de-

¹ Scott, "The Old Wood and the New," *New Phytologist*, vol. i. p. 25, 1902.

scribed, and some authors group them in two distinct genera, here adopted only as sub-genera. In addition, there are at least four undescribed forms, which appear to belong to this family; they will be further mentioned at the end of this section.

Calamopitys, Unger

Of the five published species of *Calamopitys* (in the wider sense here maintained) two, *C. Saturni*, Unger and *C. annularis* (Unger), Solms, come from Thuringia in Central Germany, one, *C. americana*, Scott and Jeffrey, from the State of Kentucky, one *C. fascicularis*, Scott, from Scotland and North England, while the fifth, *C. Beinertiana* (Goepp.), Scott, has been found both in Silesia and in Scotland.

The two species last named, *C. fascicularis* and *C. Beinertiana*, have been placed by Dr. Zalessky in a separate genus, *Eristophyton*,¹ an arrangement which has been adopted by Prof. Seward.² Here we prefer to treat *Eristophyton* as a sub-genus. The three other species, *C. americana*, *C. annularis* and *C. Saturni*, may constitute another sub-genus and be distinguished as *Eu-Calamopitys*.

While the age generally accepted for all five species is Lower Carboniferous, it is interesting to note that Solms-Laubach, in his later years, believed that the Thuringian beds, containing *C. Saturni* and *C. annularis*, were of Upper Devonian age, while he suspected the same of part at least of the Silesian Falkenberg remains.³

¹ M. D. Zalessky, "Étude sur l'anatomie du *Dadoxylon Tchiha-tcheff*," *Mém. du Comité Géol.*, nouvelle sér. livr. 68, Petrograd, 1911.

² Seward, *Fossil Plants*, vol. iii. p. 197, 1917.

³ Whether this applied to *C. Beinertiana* we cannot say. In Scotland, at any rate, there is no doubt of its Lower Carboniferous age. Solms, "Die Bedeutung der Paläophytologie für die systematische Botanik," *Mitt. der Philomath. Gesellsch. in Elsass-Lothringen*, Bd. iii. 1906. More recent work appears, however, to show that the Thuringian specimens are not older than the passage beds of the two formations.

Further, specimens of leaf-stalks apparently identical with those of *C. americana* are reported from the Genessee Shales, of Upper Devonian horizon, in Kentucky. It is therefore possible that some of the species now to be described may be even older than the base of the Carboniferous formation.

Of the three species included in the sub-genus *Eu-Calamopitys*, two, *C. annularis* and *C. americana*, are very closely allied, so that it is difficult to find distinctive characters, though, as they come from different continents, it is probable that they are really separate species. *C. Saturni* is somewhat different in structure, and apparently more advanced; it leads the way to the two *Eristophyton* species, *C. fascicularis* and *C. Beinertiana*, which certainly represent the highest type of the group.

Our account will be based, in the first instance, on *C. americana*, which is in some respects better known than its Old World fellow, *C. annularis*.

Calamopitys (Eu-Calamopitys) americana

This species was among the petrified fossil plants discovered by Prof. Charles Eastman at the base of the Waverley Shale (Lower Carboniferous) in Boyle County, Kentucky, U.S.A.¹ The nodule layer, in which the specimens occur, lies unconformably upon the Genessee Black Shale, of Upper Devonian age, but, as already mentioned, the same or a closely similar species is reported to occur at the lower horizon also.

Several specimens of the stem, of various dimensions, and also of the petioles are known; in one case leaf-base and stem have been found in connection. The stems observed range from a little over 2 cm. to about 4 cm.

¹ Scott and Jeffrey, "On Fossil Plants, showing Structure, from the Base of the Waverley Shale of Kentucky," *Phil. Trans. R.S. Ser. B*, vol. 205, p. 315, 1914.

in diameter, but the large size of some of the associated leaf-stalks shows that other stems must have attained much more considerable dimensions. The stems must have been of some height ; we have a fragment a foot long and of comparatively uniform diameter.

In the smaller stems the pith is only 2-4 mm. in diameter ; in the largest specimen observed it measures 13 mm. The word "pith," however, is not properly applicable, for it includes the primary wood, which may even extend to the middle of the stele. Outside the central region there is always a wide zone of secondary wood, accompanied on the exterior by remains of the phloem ; the cortex, with an external belt of mechanical tissue of the Sparganium type, is sometimes preserved (cf. Fig. 52). Leaf-traces are met with, passing out through the wood and cortex (Fig. 51).

We may now consider the various tissues more in detail. The main part of the primary wood consists of a ring of xylem-strands surrounding the mixed pith ;¹ the strands form collectively an almost continuous zone, and are only separated from each other, if at all, by quite narrow bands of cellular tissue. The structure of each xylem-strand is mesarch (Fig. 49), the protoxylem lying nearer the outer than the inner margin, while the centrifugal portion is usually composed of smaller tracheides than the centripetal. The tracheides, so far as the somewhat imperfect preservation allows one to judge, are for the most part of the usual form, with multiseriate bordered pits. So far, the structure appears much like that of a *Lyginopteris* with almost confluent xylem-strands. The comparison of transverse and longitudinal sections shows, however, that the tissue within the xylem-zone is not a true pith, for it contains tracheides intermixed with the short-celled parenchyma. In the smaller stems the medullary tracheides are numerous, in pro-

¹ A "mixed pith" is a pith containing tracheides as well as parenchyma.

portion to the parenchyma; where the mixed pith is larger, it is more parenchymatous, and the tracheides more scattered, occurring either singly or in little groups; they are elongated and generally resemble those of the peripheral xylem-strands; sometimes they have horizontal or slightly oblique transverse walls (Fig. 50).

It is only the peripheral xylem-strands that are concerned in the emission of the leaf-traces. It will be seen that the structure so far described is comparable to that

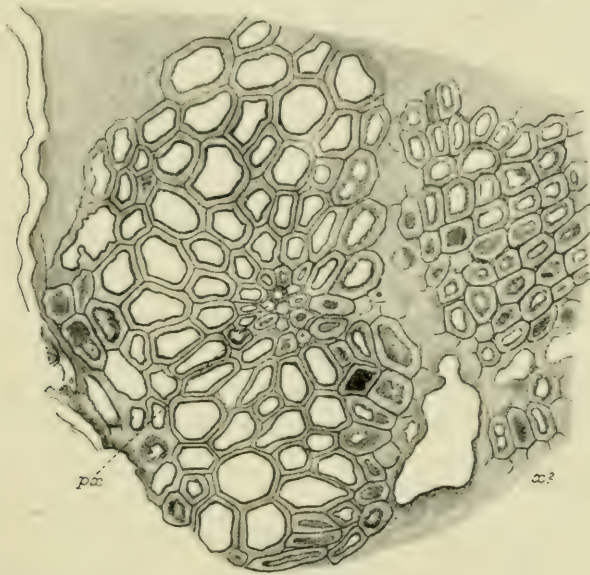


FIG. 49.—*Calamopitys americana*. Primary, mesarch xylem-strand in transverse section. *px*, protoxylem, *x²*, secondary wood. $\times 73$. S. Coll. 2862. (G. T. G. from *Phil. Trans. R.S.*)

of a *Heterangium* with a considerable amount of xylem-parenchyma, or of a *Lyginopteris*, such as *L. heterangioides*, in which some of the central tracheides still persist. The organisation may be called protostelic, in so far as xylem-elements extend to the centre of the stele, but evidently the metaxylem is becoming reduced and somewhat inconstant in its development.

In the secondary wood the tracheides are smaller than those of the primary region; the pits, where preserved, are found to be in five or six rows on the radial

walls. The medullary rays are of considerable height, and from two to eight cells in width. Portions of the cambium, phloem and pericycle are sometimes preserved, but no details of interest are shown. The secondary thickening was clearly quite normal and presents no peculiarities.

The inner cortex is a uniform tissue of short cells; the outer, mechanical zone shows the parallel bands of

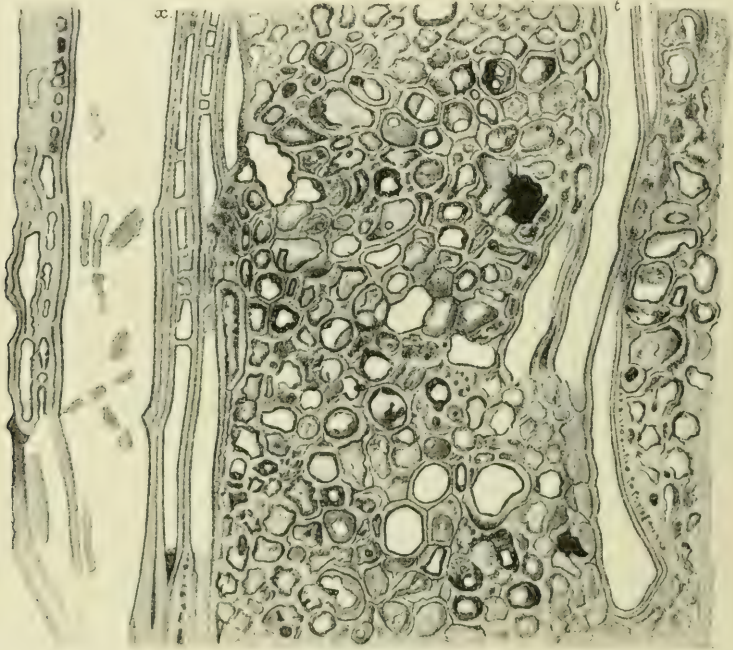


FIG. 50.—*Calamopitys americana*. Longitudinal section, showing tracheides embedded in the pith, and part of a xylem-strand. *t*, medullary tracheides; *x*, part of xylem-strand. \times about 27. S. Coll. 2867. (G. T. G., from *Phil. Trans. R.S.*)

fibres characteristic of the Sparganium cortex, and similar to those of *Heterangium*; this part of the structure is better exhibited in the petioles (Fig. 52).

The course of the leaf-trace has been followed continuously, up to the point where it leaves the secondary zone of wood. The traces succeed each other at somewhat short intervals. Where a trace is to be given off, a preliminary division first takes place, separating the xylem of the trace from a reparatory strand which remains

in the stele. This is comparable to what has been described in *Lyginopteris*. After this the trace begins to pass slowly outwards. Its xylem is at first a single strand, with one protoxylem-group, placed nearer the outer than the inner surface. The trace is accompanied, on its outer side, by a fan of secondary wood. As it gradually moves out, the protoxylem first divides and then the whole strand becomes gradually severed into



FIG. 51.—*Calamopitys americana*. Transverse section of leaf-trace, passing out through the secondary wood. The two strands are now separating, and each has a large fan of secondary xylem, beginning to encroach on the inner side. *l.t.*, *l.t.*, primary wood of the leaf-trace strands. Cortex shown to the left. \times about 7. S. Coll. 2960. From a photograph by Mr. W. Tams.

two, the corresponding arc of secondary wood also resolving itself into two distinct arcs. By the time the leaf-trace has reached the outer edge of the stelar wood, it is completely divided into two bundles, each of which is here surrounded by its special zone of secondary wood and bast, which is thicker on the outer than on the inner side (Fig. 51). Thus the leaf-trace enters the cortex as two distinct strands, each with concentric structure and secondary growth.

The further changes have not been followed in detail, but it is known that the bundles of the trace soon lose their secondary tissues and undergo further divisions, so that in a leaf-base attached to the stem there are several bundles (cf. Fig. 54). In this species, as well as in *C. annularis* and *C. Saturni*, the structure of the leaf-base has proved to be identical with that of the separate petioles, formerly named *Kalymma* by Unger, now known to be leaf-stalks of various species of *Calamopitys*. It is only in the sub-genus *Eu-Calamopitys* that the petioles are known.

The leaf-base is marked off from the cortex of the stem by a band of fibrous tissue ; it contains several vascular bundles, radially elongated as seen in transverse section. The structure is, however, best shown in the free petioles associated with the stems, and no doubt of the same species.

A fine specimen of the petiole is shown in Fig. 52, in transverse section. Its dimensions in the part figured are about 4.5×3.3 cm. There is a main ring of seventeen vascular bundles, deeply embedded in the ground tissue. On one side the bundles are large and much elongated radially ; on the opposite side they are smaller and less elongated. The two bundles at the ends of the elliptical section, and one other, are somewhat U-shaped, with the concavity outwards, and are evidently in course of division or fusion. Comparison with another transverse section shows that both processes occurred at intervals. In addition to the main vascular ring, three minute strands are present, on the inner side of the arc of large bundles, from which they have probably been given off.

Though most of the tissues of the petiole are perfect, the phloem of the bundles is so badly preserved in all cases, that it has not been possible to decide whether the structure was collateral or concentric ; the appearances point to the latter alternative. The smallest

tracheides, presumably the protoxylem, occur in groups, usually three in the larger bundles, lying embedded in the xylem near one edge. Their position is confirmed by the longitudinal sections, which in favourable cases show narrow, spiral elements not far from the edge of the xylem-strand. In the case of the minute inner bundles, there appears to be a single eccentric protoxylem. A much elongated bundle, from a still larger petiole, at least 6 cm. in diameter, shows no less than

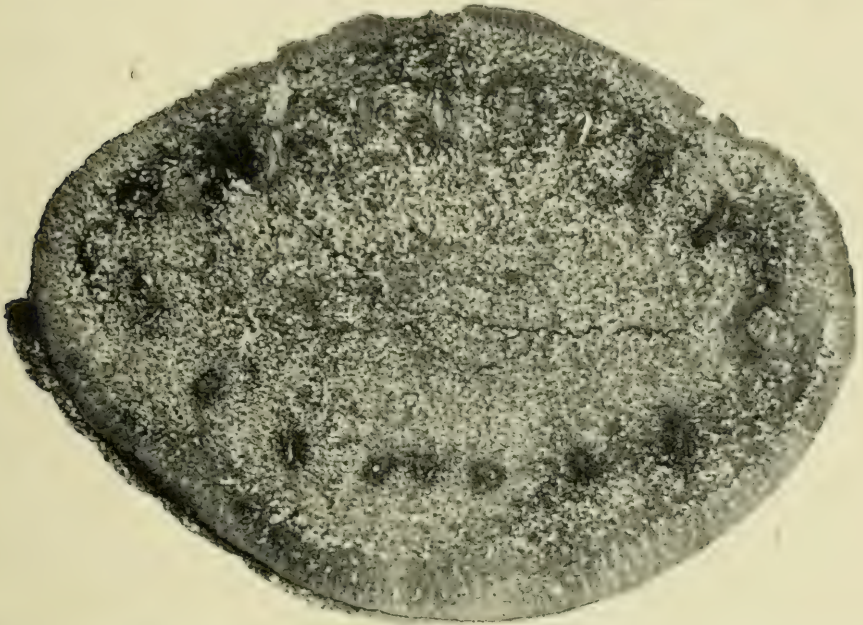


FIG. 52.—*Kalymma* (petiole of a *Calamopitys*, probably *C. americana*). Transverse section.
× about 2. S. Coll. 3046. From a photograph by Mr. W. Tams.

five protoxylem-groups in a more or less median position. The larger tracheides often have multiseriate bordered pits, as in the stem, while others are scalariform. In smaller specimens of the petiole fusion of the bundles is more frequent.

The parenchyma consists of large, short cells, and is very uniform, though the cells around the bundles are smaller. The mechanical zone of the outer cortex is beautifully developed; the radial bands of fibres are deep, and often forked outwards (Fig. 52). We may

call it a "Sparganum" cortex, for the fibrous bands on the whole run parallel, but fusion frequently occurs. Some parenchyma is present, outside the mechanical zone, but the superficial layers are not preserved.

This is the first example we have had of a petiole with very numerous bundles in a ring, a structure different from anything found in the Lyginopterideae, and necessitating the separation of the two families, though they offer many analogies in the characters of the stem. The petioles are known to have branched; in the European specimens this has been directly observed, and in the almost identical American form the specimens vary much in dimensions, so that the smaller may probably sometimes represent a secondary rachis. *Kalymma* was evidently the petiole of a large, compound frond, but no further details of its form are known. From the dimensions of the larger petioles, it is clear that the plant to which they belonged must have attained a very considerable size. It may well have been a small tree.

Calamopitys (Eu-Calamopitys) annularis

This Thuringian species, first described by Unger in 1856 as a *Stigmaria*, but recognised by Solms-Laubach in 1896 as belonging to *Calamopitys*, is so similar to *C. americana* that a brief description will suffice.

In the more typical specimens (Fig. 53), the pith, including the primary wood, has a diameter of from 7 to 9 mm. The primary xylem forms an almost continuous ring; the numerous strands of which it is built up are more or less eccentrically mesarch with the protoxylem towards the outer side; where the eccentricity is marked, the smaller, centrifugal portion consists of narrower tracheides than the more extensive centripetal region. In the pith, tubular elements are present, which are in all probability medullary tracheides, though the evidence is less conclusive in this case than in *C.*

americana.¹ In the larger specimens, the secondary wood is practically identical with that of the Kentucky species; the rays are multiseriate. In a specimen, however, from the Halle museum, referred by Solms-Laubach to *C. annularis*, the structure is somewhat different. The pith is very small (2.5×1.7 mm.) and the medullary rays of the secondary wood are narrow; most of them are uniseriate, others, or other parts of the same rays, are two cells thick, and only in one case was a width of as much as four cells observed. This is

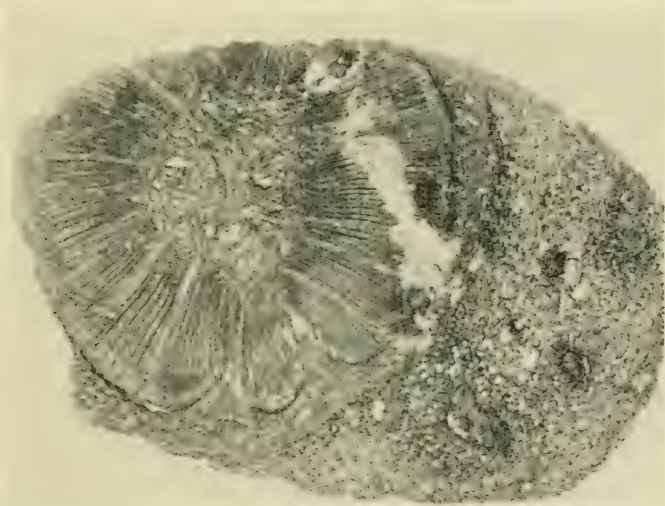


FIG. 53.—*Calamopitys annularis*. Transverse section of stem, showing primary and secondary wood, with part of cortex, and, on the right, a leaf-base, containing three bundles. $\times 24$. 413 in the Solms Coll. From a photograph by Mr. W. Tams.

a point of some importance, for comparison with species of the sub-genus *Eristophyton*, in which the rays are constantly narrow.

The course of the leaf-trace through the wood has not been followed in *C. annularis*, and we do not know at what stage it divided. Outside the wood, however, leaf-trace strands are present, with a wide secondary zone which may extend almost uniformly all round the bundle. So far the structure of the leaf-trace is essenti-

¹ Scott, "Notes on *Calamopitys*, Unger," *Linnean Society's Journal—Botany*, vol. xlv. p. 205, 1918.

ally the same as in *C. americana*. Further out, in the leaf-base, the agreement between the two species is equally close; here also the large bundles give off, towards the inner side, small subsidiary strands, each with a single protoxylem. The cortical tissues also appear to have been quite alike in the two species.

C. americana and *C. annularis* are evidently closely allied species, and appear to represent the *Calamopitys* type in its most primitive form, with an almost continuous ring of primary xylem, and medullary tracheides, indicating a protostelic structure. This last point, it is true, has only been proved in the case of the Kentucky plant, but there seems to be little doubt that the tubes in the pith of *C. annularis* are of the same nature.

Calamopitys (Eu-Calamopitys) Saturni

This is another Thuringian fossil and is the type-species of *Calamopitys*, on which the genus was founded by Unger in 1856. Our knowledge of its true structure is, however, principally due to the work of Solms-Laubach, forty years later.¹

The stems recorded are small, only reaching about 1.5 cm. in diameter; the pith is even smaller in proportion, about 1 to 2 mm., including the primary wood. The latter was described by Solms-Laubach as "an irregular tracheal zone, perhaps quite interrupted here and there, which swells out in places into expanded nests, projecting into the pith-parenchyma."² He pointed out that in *C. annularis* the primary wood was more strongly developed, forming a quite or almost closed ring.³ To judge from the stems of *C. Saturni* observed, the difference between the two species is greater than this. It will be

¹ Solms-Laubach, "Pflanzereste des Unterculms von Saalfeld," *Abhandl. der K. Preuss. Geol. Landesanstalt*, neue Folge; Heft 23, p. 63, 1896.

² Solms-Laubach, 1896, p. 65.

³ Solms-Laubach, 1896, p. 74.

seen in Fig. 54 that, surrounding the pith, there are six primary xylem-strands. Unlike the conditions in the two previous species, all the six strands are perfectly well defined and distinct from each other, just as much so as in *Lyginopteris oldhamia*; there is no approach to a continuous xylem-ring. Occasionally one of the strands is slightly embedded in the pith.

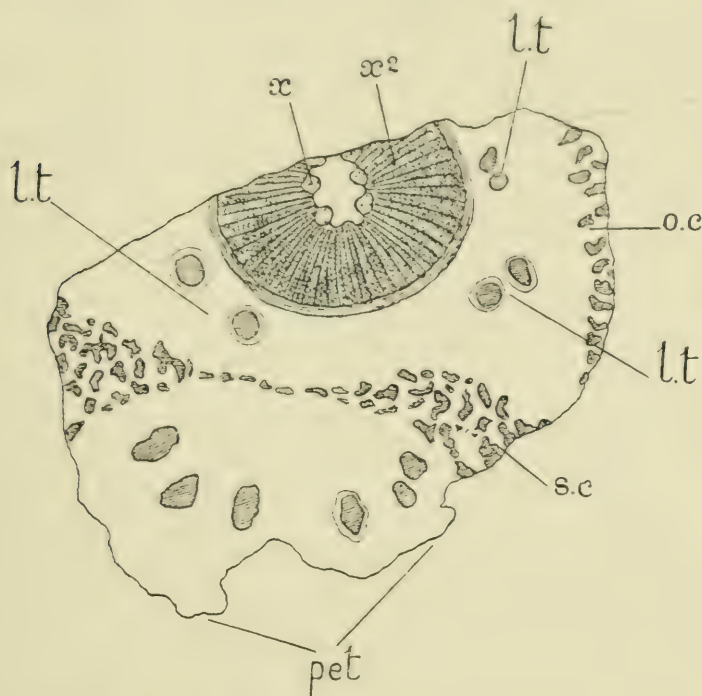


FIG. 54.—*Calamopitys Saturni*, Unger. Transverse section of stem. *x*, primary xylem-strands; *x*², secondary wood; *o.c.*, outer cortex, with fibrous strands; *l.t.*, double-leaf-traces; *pet*, petiole-base, containing six bundles; *s.c.*, sclerenchyma at junction of petiole with stem. \times about 4. After Solms-Laubach.

Another point of difference from *C. americana* and *C. annularis* is that in *C. Saturni* the xylem-strands are, as a rule, *centrally* mesarch, the centrifugal and centripetal portions being equally developed, with the protoxylem in the middle. In the preceding species the structure was *eccentrically* mesarch, with the centrifugal commonly less developed than the centripetal xylem.

Neither is there any evidence for the presence of

tracheides in the pith of *C. Saturni*; the parenchyma appears to be practically uniform and continuous. In a specimen of *C. americana* of corresponding dimensions the "pith" would be full of tracheides. For these reasons it may be concluded that *C. Saturni* is not only a perfectly distinct species, but that it stands somewhat apart from those previously described, at least as regards the primary structure of the stele.

The secondary wood, on the other hand, has essentially the same organisation as in the former species; the medullary rays are high and wide. The only difference observed is that in *C. Saturni* the rays are often dilated outwards, a feature not met with in the other two species. The phloem is sometimes preserved, and was found by Solms-Laubach to contain bast-fibres as well as the usual elements of the soft bast.

The outward course of the leaf-trace was followed by Solms-Laubach with great accuracy. It differs from that described in *C. americana*, for in *C. Saturni*, though the outgoing strand doubles its protoxylem-group in traversing the secondary wood, the trace itself remains undivided, and enters the cortex as a single bundle. It is only in the cortex that the division into two strands takes place. On leaving the stele, the undivided trace has secondary tissues of its own, but they are limited to the outer side. The two bundles resulting from the first division of the leaf-trace divide again, and of the four strands thus formed the two lateral ones repeat the process, so that the leaf-base contains six bundles, a number which, in the small specimens observed, is still maintained in the free petiole (Fig. 54).

The bundles in the leaf-base have lost their secondary tissues and acquired in all respects the same structure as in the leaf-base and petiole of the species previously described. From the arrangement of the successive leaf-traces, which follow one another at short intervals, so that five may appear in the same transverse section,

Solms-Laubach determined the phyllotaxis as $\frac{2}{5}$ or a very similar higher fraction.

Besides the late division of the leaf-trace, we have seen that *C. Saturni* is characterised by the distinct strands of primary xylem, by their centrally mesarch structure, and probably by the absence of medullary tracheides.

As regards the structure of the leaf-base and petiole, all the three species of *Eu-Calamopitys* appear to be essentially alike. In all, the petiole is a *Kalymma*, with a Sparganium outer cortex and a single main ring of bundles, each of which has internal protoxylem-groups. We are not yet in a position to distinguish between the petioles of the three species. Yet there can be no doubt that under the name *Kalymma* several species are included. The distinctions are not of sufficient moment to be dwelt on here.

We may, however, call attention to certain petioles, which have been provisionally placed in a separate genus, *Calamopteris*, Unger. A Thuringian species, *C. debilis*, Unger, differs but little from the smaller petioles referred to *Calamopitys americana*, except that the indications point to a collateral structure of the bundles.¹ The Kentucky species, *C. Hippocrepis*, Scott and Jeffrey, is more distinct. Here the bundles are extensively fused, though some remain separate, the ring having the form of a kind of split horse-shoe, with a wide opening on one side, and a narrower gap on the other. The arrangement of the bundles remains fairly constant in different transverse sections, though the narrower gap may close up. The phloem is tolerably preserved, and seems to be limited to the outer side of the vascular ring, the structure thus being collateral. The xylem consists,

¹ Scott and Jeffrey, *l.c.* 1914, p. 330; R. Richter and F. Unger, "Beitrag z. Paläontologie des Thüringer Waldes"; 2ter Teil, von F. Unger, "Schiefer- u. Sandsteinflora," *Denkschriften der K. Akad. d. Wiss., Wien*, Bd. xi. 1856.

so far as observed, of scalariform tracheides, and has mesarch structure, the protoxylem-groups lying towards the outer surface. The ground-tissue is like that of *Kalymma*, and the mechanical zone is strongly constructed, with the fibrous bands near together.

The fossil is evidently a petiole, allied to that of *Calamopitys*, but differs sufficiently to be kept distinct. It may probably have belonged to some unknown stem of the family Calamopityeae.

The Sub-genus Eristophyton

We now come to the two species which were separated by Dr. Zalesky from *Calamopitys*, under the name *Eristophyton*, here adopted as a sub-genus. The systematic position will be discussed after the species have been described. Unfortunately, in the case of both species, the cortical tissues and leaf-base are unknown, so that our data are much more restricted than in *Eu-Calamopitys*, a fact which may account for the difference of opinion as to the relations of these plants.

Calamopitys (Eristophyton) fascicularis

Two specimens of the plant are known. One was derived from the Calciferous Sandstones of the Kilpatrick Hills in Dumbartonshire, the other from the Carboniferous Limestone of Haltwhistle in Northumberland; ¹ thus both are of Lower Carboniferous age. The actual specimens are from 2 to 3 cm. in diameter, but these dimensions are of no significance, as even the wood is incomplete.

The pith is small, from 2 to 3 mm. in diameter. It is surrounded by a ring of eight or nine primary xylem-

¹ Scott, "On the Primary Structure of certain Palaeozoic Stems with the *Dadoxylon* Type of Wood," *Trans. Royal Soc. Edinburgh*, vol. xli. Part ii. 1902.

strands, beyond which is the zone of dense secondary wood (Fig. 55). The strands around the pith are of very unequal size, the larger having a diameter of 0.8 – 1 mm., while the smallest measure less than 0.25 mm. The comparison of successive transverse sections shows

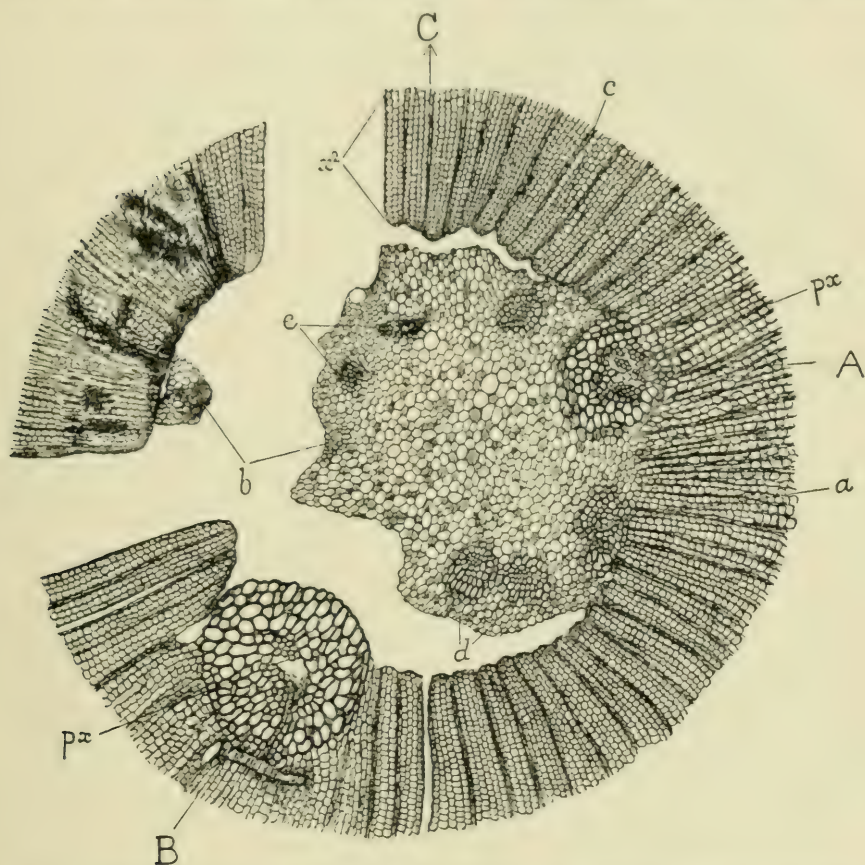


FIG. 55.—*Calamopitys fascicularis*. Transverse section of central part of stem, showing the pith (rather contracted), the primary xylem-strands, and part of the secondary wood. A, large xylem-strand, about to pass out to a leaf; B, still larger strand, already on the way out; px, protoxylem-groups; C (arrow), direction of another outgoing strand; a, b, c, reparatory strands of the bundles A, B, C. d, e, main and reparatory strands of two other leaf-traces, lower down in their course. $\times 20$. Kidston Coll. 540A. (G. T. G.)

that the large bundles are those which are seen in the upper part of their course, where they are about to pass out as leaf-traces (Fig. 55, B) while the smaller strands are those cut at a lower level. Traced downwards, the strands rapidly diminish in size. Another feature which will be noticed is that the largest xylem-strands are in

immediate contact with the secondary wood, while all the others are more or less embedded in the pith, a few layers of small-celled parenchyma intervening between these strands and the inner edge of the woody zone (Fig. 55, *c*, *d*, *e*).

The large, outgoing xylem-strands are almost circular in section and centrally mesarch, agreeing exactly in structure with those of *Calamopitys Saturni*. The central protoxylem is accompanied by a little thin-walled tissue. The larger primary tracheides are of the usual kind with multiseriate pits, while the elements adjoining the protoxylem are smaller and scalariform.

The xylem-strands lower down in their course, as they dwindle in size, change somewhat in structure; the protoxylem approaches the inner edge of the strand, the centripetal xylem becoming reduced and even interrupted (Fig. 55). There is thus, as the xylem-strand is followed downwards, an approach to endarch structure; nothing of the kind is found in any species of *Eu-Calamopitys*. The reduction of the centripetal xylem, though here so local, marks a first step towards the structure of the higher Gymnosperms, in which it ultimately dies out. On the other hand, the great size of the outgoing primary strands, often amounting to $\frac{2}{3}$ of the pith-diameter, is a character indicating that we are here still among plants of Pteridosperm affinity.

The pith itself consists of short-celled tissue; a few of the cells have dark contents and may possibly have been differentiated for some special function, such as secretion. There is nowhere any indication of medullary tracheides.

The secondary wood is very different from that of any of the *Eu-Calamopitys* species, if we except the peculiar specimen of *C. annularis* described above (p. 117). In *C. fascicularis* the wood is dense, with small tracheides and narrow rays, usually one cell in width, but occasionally biseriate in the middle. The rays are also low, seldom

exceeding about sixteen cells in height. The bordered pits of the tracheides are excellently preserved; they are usually in three or four rows on the radial walls, and their arrangement in vertical series is more regular than in *Eu-Calamopitys*. In form they are more or less hexagonal, owing to their close contact and alternate position.

The most remarkable feature of the secondary wood in this species is the structure of its inner layers, where it borders on the pith and primary strands. In this region the tracheides are short and wide, with more numerous rows of pits on their walls; their arrangement is irregular and the medullary rays between them are correspondingly distorted. The structure of this inner part of the secondary wood is comparable to that of the primary xylem in *Megaloxylon* (p. 102) and may also have served the purpose of water-storage. This function may have been the more necessary, as the xylem-strands dwindled so much in the lower part of their course that a reserve of water may have been required to maintain the supply.

The course of the leaf-traces has been followed, within the narrow limits imposed by the incompleteness of the specimens. From the succession of the leaf-traces it is clear that the phyllotaxis was $\frac{2}{3}$. From the rapid succession of the leaf-traces it may be inferred that the internodes were short. Otherwise the course of the traces, and especially the union of each in turn with the strand on its cathodic side, agree perfectly with the conditions in *Lyginopteris oldhamia* (cf. p. 31).

As the trace passes out through the woody zone, its protoxylem divides into two groups. No doubt this was preparatory to the division of the trace as a whole, but the loss of the outer tissues prevents our following up its further course.

The chief points to be noted in *C. fascicularis* are as follows: The centrally mesarch structure and large

size of the outgoing xylem-strands, resembling those of *C. Saturni*; their rapid attenuation and approach to endarch structure as they pass downwards, and their becoming embedded in the pith; the course of the bundles, agreeing, so far as can be determined, with that in *Lyginopteris oldhamia*; the structure of the secondary wood, with its low and narrow rays, like the wood of the Cordaiteae (see p. 273) and certain Conifers.

Calamopitys (Eristophyton) Beinertiana

This fossil is the *Araucarites Beinertianus* of Goeppert, who first recorded it as long ago as 1850. It was re-described by Solms-Laubach in 1893, but the primary structure was not observed till 1902.¹ The original specimens came from deposits, almost certainly of Lower Carboniferous age, near Falkenberg in Silesia, and at a later date the same species was identified by Dr. Kidston in the Calciferous Sandstones of the Tweed. Subsequently specimens were observed in the neighbourhood of the Balaton See in Hungary. Thus the species had a wide distribution at the beginning of the Carboniferous period.

The stem is larger than that of *C. fascicularis*; in the Scottish specimens, though incomplete, the diameter is about 5 cm. With the exception of a fragment of scale-bark, nothing beyond the pith and wood is preserved. The pith is considerably larger than in *C. fascicularis*, the diameter being about 8 cm. in Solms-Laubach's Falkenberg specimen and 13-15 cm. in the Tweed fossil. A remarkable feature in the structure of the pith is the presence of large sclerotic nests, with radiating cells around them, the whole strikingly like the nests in the pith of *Lyginopteris oldhamia*. This cannot, however, be accepted as evidence of affinity, for the character is only a specific one, the nests

¹ Scott, *l.c.* 1902, p. 341.

being entirely absent even from the closely allied *C. fascicularis*.

Surrounding the pith is a ring of numerous strands of primary xylem, which may be locally confluent with one another. The largest strands are those which are about to pass out as leaf-traces; they have the same centrally mesarch structure as in the preceding species; the dimensions also are nearly equal, the diameter amounting to 0.8 mm., but they appear less important owing to the greater size of the pith. The smaller strands represent the same bundles lower down in their course. As they pass downwards they gradually lose their centripetal xylem, and thus become endarch; the change of structure, which was only imperfectly carried out in *C. fascicularis*, is here complete. The strands, in this species, remain in contact with the woody zone and do not become embedded in the pith.

The phyllotaxis has not been determined, but was no doubt a complex spiral. Several leaf-traces may appear in the same transverse section, as they pass out through the wood, so we may infer that the internodes were short. The traces, observed in their passage through the secondary wood, do not clearly show any division of the protoxylem, and nothing is known of their ultimate fate.

The wood, as in *C. fascicularis*, has a dense structure, like that of a Cordaitean or Araucarian stem. The medullary rays are seldom more than one cell in width; they vary much in height. The bordered pits are usually in two rows on the radial walls of the tracheides; in places they may be reduced to a single series. The secondary tracheides thus present a sharp contrast with the large elements of the primary xylem-strands, in which the rows of pits may be very numerous. The short, inner, secondary tracheides, characteristic of *C. fascicularis*, have not been observed in the present species.

We have scarcely any information about the roots of *Calamopitys*. It is therefore of interest to note that Solms-Laubach found, in the Falkenberg material, fragments of roots associated with *C. Beinertiana*, and agreeing with the stem sufficiently, in the structure of the secondary wood, to be referred with some probability to the same species. One of these associated roots had a clearly pentarch primary xylem.¹

C. Beinertiana has much in common with *C. fascicularis*, both in its primary and secondary structure. The former species, however, seems to be somewhat the more advanced of the two, as shown especially by the fact that the xylem-strands, as traced downwards in the pith, actually assume an endarch condition, a structure to which the corresponding strands of *C. fascicularis* show only an approximation. The large size and peculiar structure of the pith give the stem a very different anatomical character from that of the allied species. In general appearance the sections of *C. Beinertiana* suggest the organisation of the higher Gymnosperms more strongly than those of any other species so far referred to *Calamopitys*.

SYNOPSIS ²

A concise synopsis of the chief characters of the five species may be of service for reference.

1. Xylem-strands of fairly uniform size, all mesarch (*Eucalamopitys*).

Rays usually multiseriate.

Petiole with *Kalymma* structure.

A. Xylem-strands usually eccentrically mesarch, with protoxylem outwards, connected to form a nearly continuous zone. Medullary tracheides present.³

C. americana (from Kentucky).

C. annularis ⁴ (from Central Germany).

¹ Solms, *l.c.* 1893, p. 208.

² Scott, *l.c.* 1918, p. 221.

³ Proved for *C. americana*; highly probable for *C. annularis*.

⁴ It would be premature to give distinctive characters at present. In the meantime the localities prevent any confusion.

B. Xylem-strands usually centrally mesarch ; quite separate from one another. Medullary tracheides probably absent. *C. Saturni*.

2. Xylem-strands of very unequal size ; large and centrally mesarch in the upper part of their course, becoming small and nearly or quite endarch lower down (*Eristophyton*).

Rays usually uniseriate.

(Petiole unknown.)

a. *C. fascicularis*. Pith small, with no sclerotic nests.

Smaller xylem-strands embedded in the pith, with their centripetal xylem much reduced.

β. *C. Beinertiana*. Pith large, with conspicuous sclerotic nests.

All xylem-strands in contact with secondary wood.

Centripetal xylem dying out in the smaller strands, which thus become endarch.

The course of the leaf-trace has not been included in the synopsis as it is only adequately known in the two species *C. americana* and *C. Saturni* ; in the former the first division of the trace takes place in the zone of thickening ; in the latter not till the trace has passed beyond this zone.

Affinities of Calamopitys

The question whether we regard *Eristophyton* as a separate genus, or as a sub-genus under *Calamopitys* is of little importance. We have rather to consider how far the five species described form a natural series and what affinity they show to other groups.

The three species grouped under *Eu-Calamopitys* are undoubtedly allied ; they agree in the constant mesarch structure of the xylem-strands throughout their whole course, in the organisation of the leaf-base and petiole, in all cases of the *Kalymma* type, and in the general character of the secondary wood, which if we except the peculiar specimen of *C. annularis* referred to above (p. 117) always has wide medullary rays.

Within this group, *C. americana* and *C. annularis* present a closer agreement, shown in the prevailing

eccentrically mesarch structure of the primary xylem, the centrifugal portion being the less developed, in the union of the primary strands to form an almost continuous zone, and probably in the presence of medullary tracheides, rendering the structure protostelic. The last character is as yet less certainly demonstrated in the case of *C. annularis* than in that of its fellow species.

C. Saturni, on the other hand, appears to stand somewhat apart; here the xylem-strands are, as a rule, centrally mesarch, and are also quite separate from one another; neither is there any evidence for the presence of tracheides in the pith. In these respects *C. Saturni* approaches the *Eristophyton* species.

The sub-genus *Eristophyton* is, however, distinguished from *Eu-Calamopitys* by characters of considerable importance. The gradual dwindling of the xylem-strands as they pass down the pith, accompanied by the reduction or even complete suppression of the centripetal portion, is a striking feature, peculiar to this sub-genus. The latter character marks an approach, as far as it goes, to the total loss of the centripetal wood, which characterises the higher Gymnosperms. We find a familiar intermediate stage in the recent Cycads, where the centripetal xylem has wholly disappeared in the main stem and even in the leaf-base, while it still persists in the petiole and lamina, and occasionally in the floral peduncle.

The characters of the primary xylem are those on which the distinctness of the *Eristophyton* group seems to me chiefly to depend. Another feature, also of importance, on which Dr. Zalesky has laid the main stress, is the structure of the secondary wood, which in *Eristophyton* is constantly of the type found in Cordaiteae and certain Conifers, with narrow and comparatively low rays, while in *Eu-Calamopitys* it is, as a rule, of a more Lyginopteridean character, with the rays high and wide. In this point also the *Eristophyton* species

show an obvious approach to the organisation of the higher Gymnosperms.

There is thus a considerable range of structure within the genus *Calamopitys*, in the wide sense, and Dr. Zalesky's separation of *Eristophyton* as a distinct genus has much in its favour. But on the whole I agree with Solms-Laubach¹ that, while our knowledge of the structure is so incomplete, it is wisest to avoid the multiplication of genera. The true relations of *Eristophyton* to *Eu-Calamopitys* will only be determined, when we become acquainted with the cortex and petiole of the former, so as to be in a position to compare the whole structure of the two groups. Until then, any arrangement must be provisional.

In the meantime, judging from our present limited knowledge, it seems clear that the five species form a natural series, in which *C. americana* and *C. annularis* are the most primitive members, and *C. Saturni* in some respects intermediate, while *C. fascicularis* and *C. Beinertiana* are decidedly the most advanced, the last-named having made the maximum progress in a Gymnospermous direction. The principal reason for still including the *Eristophyton* species in *Calamopitys*, and therefore in the Pteridosperms or Cycadofilices,² is the structure of the outgoing leaf-trace, which exactly resembles a xylem-strand of *C. Saturni* and is unlike that of any other known plant. The great relative size of the primary strand, as it leaves the pith, so marked in *C. fascicularis*, is a feature peculiar to Pteridosperms (if we leave the Ferns out of consideration) and is totally unlike anything met with in the higher Gymnosperms. In *C. Beinertiana*, where the pith is so much larger, this character is less conspicuous, but the affinity of these two species is not

¹ Solms-Laubach, Review of Zalessky, *Zeitschrift f. Botanik*, Band iv. 1912, p. 291.

² Dr. Zalessky expressed some doubts as to the relation of *Eristophyton* to this class.

disputed. We may presume that in *Eristophyton*, as in *Eu-Calamopitys*, so massive a leaf-trace supplied a large, and probably a compound leaf.

As regards the affinities of the genus and family as a whole, it is fairly clear that the nearest relationship is with the Lyginopterideae. *C. Saturni* admits of a ready comparison with *Lyginopteris*, both having a ring of distinct mesarch xylem-strands surrounding the pith. The secondary wood is also very similar; and the course of the leaf-traces analogous. Now, however, that it has been discovered that some species of *Calamopitys* were protostelic, a comparison with *Heterangium* becomes more apposite. There is evidently a somewhat close analogy between *C. americana*, for example, and *Heterangium*, especially such species of the latter as had several vascular bundles in the petiole. But there is nothing to indicate a direct connection between the two families, nor are there any grounds for deriving the one from the other. The Calamopityeae and the Lyginopterideae are parallel lines, so far as we can trace them; if our knowledge ever extends further back, we may find that they had a common origin in some earlier period.

There is no other group with which any near relationship is shown. The more advanced species of *Calamopitys*, forming the sub-genus *Eristophyton*, make some approach, as already mentioned, to the higher Palaeozoic Gymnosperms, namely the Cordaitales. The significance of this approximation will be better appreciated after we have described some other forms.

NEW CALAMOPITYEAE

As already mentioned, there are four plants of Carboniferous age still undescribed which appear to have a more or less close affinity to the family Calamopityeae. I am indebted to my friend Dr. Kidston for the opportunity of examining and describing these fossils, all of which

are his discoveries. A full description with figures will be given elsewhere—here it is only proposed to characterise the new forms briefly.

1. *Calamopitys zonata*, Kidston.—This is a provisional name which will probably require alteration as regards the genus. The fossil is of Lower Carboniferous age, coming from the Carboniferous Limestone Series of Ayrshire. The specimen, which was collected by the late Dr. John Young, is part of a fairly large stem about 6 cm. in diameter, including the cortex. Around the large pith a certain number of primary xylem-strands are distributed; their structure appears to be endarch throughout. The secondary wood is dense, with unusually low, uniseriate, or locally biseriate rays. It is remarkable for having distinct annual rings. The cortex, as preserved, is mostly secondary, consisting of successive zones of periderm.

The structure of the secondary wood removes the plant from *Eu-Calamopitys*; it might perhaps be referred to the sub-genus *Eristophyton*, but if, as appears to be the case, the xylem-strands are constantly endarch, an affinity with Zalessky's genus, *Mesopitys*, mentioned in another connection (p. 283) may be indicated.

2. *Calamopitys radiata*, sp. nov.—The specimen is derived from the Calciferous Sandstone Series of Dumbartonshire, and is thus somewhat older than *C. zonata*. It presents quite different characters from that species. The pith is small, and is surrounded by a ring of partly confluent xylem-strands, which are either actually exarch, or slightly mesarch, with the protoxylem very near the outer edge. There appear to be tracheides scattered in the pith, and in the case of a small branch borne on the main stem the appearance suggests that such elements were numerous, as in the smaller specimens of *C. americana*. But in the absence of good longitudinal sections through the pith, the presence of medullary tracheides cannot be regarded as finally proved.

The secondary wood is very parenchymatous, owing to the enormous dilatation of some of the medullary rays. These enlarged rays are crossed in various directions by strands of tracheides and present a fantastic appearance in tangential section. No cortex is present.

There seems to be no objection to putting this species in *Calamopitys* and in the sub-genus *Eu-Calamopitys*. The xylem-strands in *C. annularis* are sometimes nearly exarch, and it is with this species that the affinity seems to be closest. The great size and peculiar structure of certain of the medullary rays characterise the species as a perfectly distinct one.

The two remaining forms are referred to a new genus, *Bilignea*, Kidston, which is of great interest. Its essential character lies in the fact that the pith is replaced by a more or less solid column of short tracheides.

3. *Bilignea solida*, Kidston.—The fossil comes from the Carboniferous of Ayrshire, but its horizon is not further known. The cortex is absent, but the inner tissues are remarkably perfect. The central column consists exclusively of very short, rather wide tracheides, with numerous bordered pits on their walls.

The central tracheal column is surrounded by a ring of xylem-strands which pass out to form the leaf-traces. These strands are mesarch in the upper part of their course, the centripetal xylem being predominant; lower down, this portion is gradually reduced till the dwindling strand becomes nearly or quite endarch, as in the *Eristophyton* species of *Calamopitys*. The xylem strand begins to divide into two before passing out. The internodes are short and the phyllotaxis probably $\frac{5}{13}$. The secondary wood is dense, with low, uniseriate, or locally biseriate rays. The specimen was collected by Mr. John Smith, Dalry.

4. *Bilignea resinosa*, sp. nov., from the Calciferous Sandstone Series of Dumbartonshire. This Lower Carboniferous species differs in several respects from *B.*

solida. In particular, the tracheides of the central column are intermingled with large "secretory sacs"; the xylem-strands are smaller than in *B. solida*, and show no sign of division; they are mesarch on entering the wood, becoming apparently endarch and then dying out, as traced downwards.

A *Biligneæ* may be described as an *Eristophyton* in which the pith-cells are replaced by short tracheides. The new genus provides us with fresh examples of the utilisation of the central column for the purpose of water storage, but, whether in this case the storage-apparatus was derived directly from a protostele, or by the transformation of a pre-existing pith, must be left an open question.

STENOMYELEAE

Stenomyelon, Kidston

This genus now contains two species, *Stenomyelon tuedianum*, Kidston, and *S. tripartitum*, Kidston, both of Lower Carboniferous age and derived from the Calcareous Sandstone series of southern Scotland.

Stenomyelon tuedianum, Kidston

This is the type-species, on which the genus was founded by Dr. Kidston. The fossil, which is of great interest, has a curious history. The original specimens were discovered by Mr. Adam Matheson, of Jedburgh, in the fifties of the last century, but no description was published. Dr. Kidston, on examining the specimens, suspected, from the character of the matrix, that they came from the Norham Bridge locality, on the Tweed. In 1901, together with Mr. Macconochie of the Scottish Geological Survey, he carried out a careful search, which was rewarded by the discovery of the material sought

for, in a cutting in the road at the north end of Norham

Bridge. The block then found yielded the beautiful specimen on which the memoir by Kidston and Gwynne-Vaughan is chiefly based, though supplemented by a comparative examination of the original material.¹

The cortex of the stem is much flattened, giving the fossil a winged appearance, which the plant did not possess in the natural condition; the stele, however, retains its approximately cylindrical form (Fig. 56). In the principal specimen, the stele, measured to the outside of the secondary wood, is 8 to 9 mm. in diameter, while the bluntly triangular primary xylem is from 3 to 4 mm. The latter consists of three masses or lobes, more or less separated from one another by narrow bands of cellular tissue, meeting at the centre, and forming collectively the "narrow pith" recorded in the name of the



FIG. 56.—*Stenomyelon tuedianum*. Transverse section of the stem, showing the cylindrical stele, the cortex flattened into a thin wing, and other fragments. The dividing leaf-traces are seen at various points. $\times 2\frac{1}{2}$. Kidston Coll. 2068. From Kidston and Gwynne-Vaughan.

¹ Kidston and Gwynne-Vaughan, "On the Carboniferous Flora of Berwickshire, Part I. *Stenomyelon tuedianum*, Kidston," *Trans. Royal Soc. Edinburgh*, vol. xlviii. part ii. 1912.

genus¹ (Fig. 57). The leaf-traces were given off from the ends of the lobes, and it is inferred that the leaves were borne in three vertical rows, for the lobes retain their individuality throughout. The zone of secondary wood is thickest opposite the bays of the primary xylem, and thinnest at its prominent corners, thus assuming a practically circular transverse section. In the collapsed cortex, numerous leaf-trace bundles, in various stages of subdivision, are met with; the outer cortex is of the familiar *Sparganum* type (Fig. 56). Portions of detached leaves accompany the stem.

Returning to the primary wood of the stem, we find that the three xylem-lobes contain no parenchyma, each lobe consisting of a solid mass of tracheides. The cellular bands between the xylem-lobes are usually not quite continuous, but often interrupted by bridges of tracheides. Yet, on the whole, the lobes, though thus connected locally, retain their independence. In addition to the bands between the lobes, there is often a little parenchyma separating the primary wood from the surrounding secondary zone.

The large tracheides of the primary xylem are elongated elements, reaching 160 μ in diameter, with the usual multiseriate bordered pits. The outermost elements of each lobe, however, are scalariform, and diminish in size. There appears to have been no protoxylem proper to the stem, but where a leaf-trace is about to depart from the distal end of a lobe, a pair of definite, exarch protoxylem-groups appear. These groups are decurrent from the leaf-trace, and unite to form a single strand lower down in the stem, ultimately disappearing altogether. It will be remembered that in *Megaloxylon* the protoxylem was limited to the leaf-traces (p. 104).

The structure of the secondary wood presents no exceptional features. The medullary rays are as a rule of considerable height, and from one to six cells in width ;

¹ The nature of these bands is discussed below, p. 144.

the tracheides are smaller than those of the primary region, but vary in size in different zones; they have from three to five rows of crowded bordered pits on their radial walls only. Early stages of the development of the secondary wood have been observed; it began to form in the bays of the primary xylem, and subsequently extended round the prominent angles.

No true phloem is preserved, but outside the wood a radially seriated tissue is present, which, when seen in transverse section, may simulate phloem (Fig. 57). That it can hardly be of that nature is indicated by the fact that its cells are quite short, and that no medullary rays can be distinguished. Kidston and Gwynne-Vaughan interpret this tissue as an internal periderm. A comparison also suggests itself with the sclerotic layers of the phloem in *Protopitys Buchiana*, described by Solms-Laubach; they also have short cells and show no medullary rays (see below, p. 152). In *Stenomyelon*, however, no trace of the intervening layers of soft bast is found. Sclerotic nests, quite similar to those in the pith of *Calamopitys Beinertiana*, are frequent in the inner cortex, and are often found in close connection with the periderm or hard bast. Otherwise little of the structure of the inner cortex is preserved. The outer cortex is of the usual *Sparganium* character, with parallel, vertical bands of fibres, which seldom unite with one another. The tissue between the fibrous bands is a rather firm-walled parenchyma, containing cells with dark contents, possibly representing resin-sacs.

“The leaf-traces,” to quote from Kidston and Gwynne-Vaughan, “depart from the ends of the lobes of the primary xylem in a perfectly protostelic manner” (*l.c.* p. 266). The traces are given off in regular succession from the three lobes. The extremity of one of the lobes gradually becomes more prominent, and is then nipped off as a fairly large, roundish leaf-trace (Fig. 57) leaving no gap behind. The trace, with its two exarch

protoxylem-groups, passes slowly outwards, the secondary wood at once closing in at the rear. When it first frees itself from the stele, the trace has its own zone of secondary wood, extending all round, but considerably more

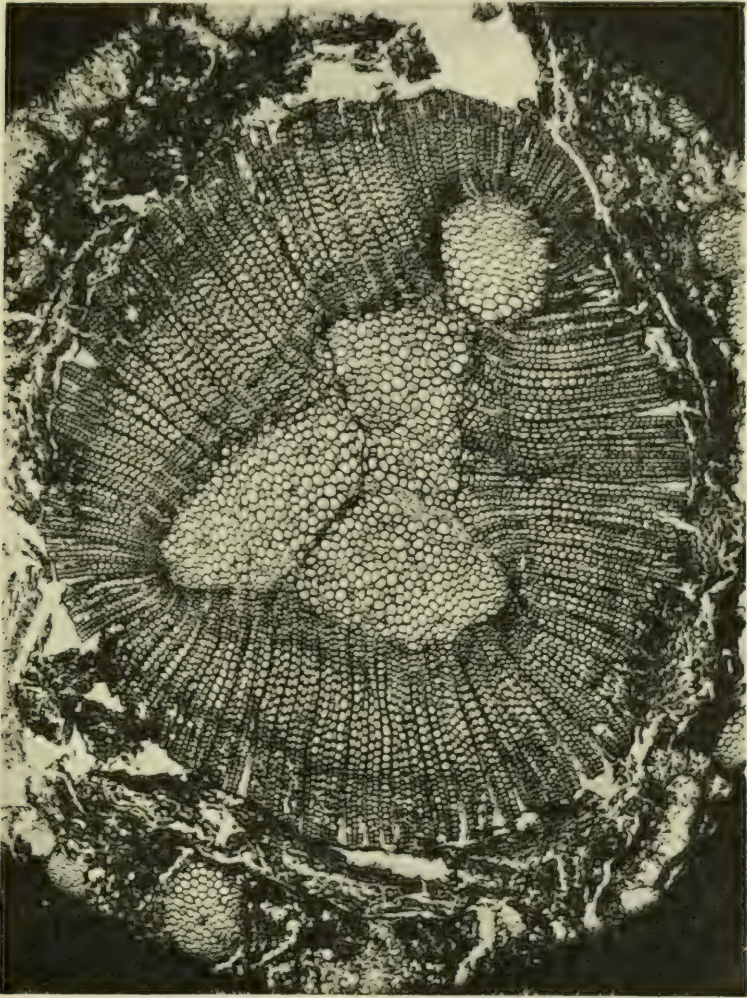


FIG. 57.—*Stenomyelon tuedianum*. Transverse section of stele and adjacent tissues, showing a leaf-trace just free from the primary xylem. $\times 9$. Kidston Coll. 2095. From Kidston and Gwynne-Vaughan.

developed on the outer than on the inner side (Fig. 57). The double protoxylem may be regarded as a preparation for the first division of the trace, which soon follows, each of the resulting strands having a single protoxylem. The secondary tissues persist, at least on the abaxial

side of each strand, till after the first division, but subsequently disappear. The subdivision of the trace continues, each successive division being preceded by a bipartition of the protoxylem. The position of the latter changes after the trace has left the stele. At first, as we have seen, it lies on the outer edge of the xylem-strand, which is thus exarch, but soon it becomes immersed, rendering the structure

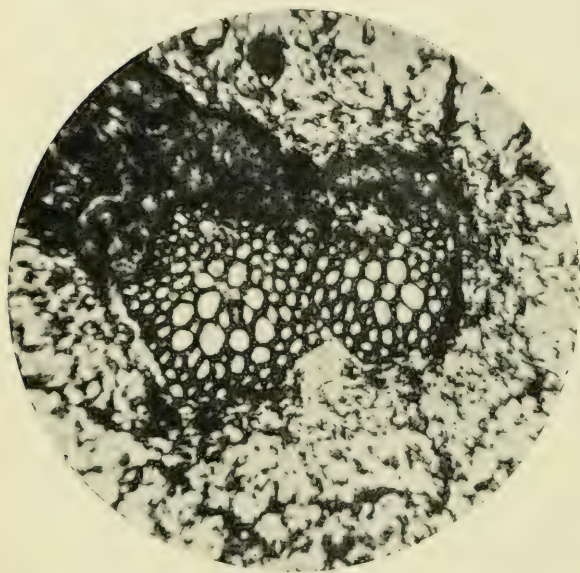


FIG. 58.—*Stenomyelon tuedianum*. Leaf-trace in the cortex in course of division, showing the two immersed protoxylem-groups. $\times 36$. Kidston Coll. 2097. From Kidston and Gwynne-Vaughan.

of the free trace-bundles slightly mesarch (Fig. 58). The strands of the subdivided trace are much displaced, but there is no doubt that the protoxylem was directed outwards in all cases.

In the flattened portions of petiole and rachis associated with the stem the bundles are very numerous. They retain the structure already described, but the

scalariform elements are relatively more abundant than in the stem; they may extend all round the strand, but are chiefly concentrated in the side where the protoxylem is placed. The size of the largest leaf-stalk is out of proportion to that of the associated stem; probably it belonged to a larger specimen. The Sparganum cortex is much more strongly developed on the petiole than on the stem.

The size of the stems varied considerably; in one specimen the diameter of the stele, including a certain

amount of secondary wood, is only 2.5 mm. as against 8 or 9 mm. in the principal specimen. These variations suggest that the stem may have branched.

Associated with the stem, sections of a midrib and lamina have been observed. From their large size it was conjectured by Kidston and Gwynne-Vaughan that the leaf may probably have been a simple one.

Before considering the affinities of *Stenomyelon* it will be desirable to give some account of the second species, *S. tripartitum*, which has not hitherto been described.

Stenomyelon tripartitum, Kidston

This species is derived from the Calciferos Sandstones of the Langton Burn, near Duns, Berwickshire. I am indebted to the discoverer, Dr. Kidston, for the loan of the sections which he had cut, and for permission to describe the plant. It is hoped to publish a fuller account elsewhere.

There are three distinct specimens known, besides some fragments; in none of them is anything shown beyond the wood. The diameter ranges from 1 cm. to 3 mm. The size of the primary xylem varies greatly, its diameter in the three stems being about 3 mm., 1.25 mm., and 0.7 mm. respectively. In the larger stems the three lobes of the primary xylem are widely separated, but this is no doubt partly due to accidental causes.

The primary tracheides are comparable in size to those of *S. tuedianum*. The outer tracheides are somewhat smaller, but the protoxylem could not always be detected, nor is the emission of a leaf-trace shown, in any specimen. The secondary wood consists of tracheides about 75 μ in diameter, with numerous medullary rays of varying width.

Longitudinal sections show that the large primary tracheides have four or five rows of bordered pits on their walls, while the smaller peripheral elements are

scalariform or even spiral, with transitions to the pitted form. The tracheides of the secondary wood have three or four rows of pits on the radial walls, while the rays present the usual muriform appearance. Tangential sections show that they are in a large proportion of cases uniseriate, and often of small height, even down to a single cell.

The smallest specimen is a minute stem, the total diameter of the wood barely reaching 3 mm., while the maximum diameter of the primary region is only about 0.7 mm. The most interesting feature is that the primary xylem of this small stem or branch is quite undivided, and consists, so far as can be judged from the transverse section, of a continuous mass of tracheides. The tripartite xylem is therefore not a constant character of the species. The primary xylem has no marked lobes, but there are three angles, at one of which a protoxylem-group is fairly evident.

There are five transverse sections in all, of the various specimens, and in none of them is the emission of a leaf-trace from the stele shown. This is rather a striking difference from *S. tuedianum*, in which, as Dr. Kidston informs me, "it is almost impossible to get a section without evidence of leaf-traces going off." It would thus seem that the internodes of *S. tripartitum* must have been considerably longer than those of the type-species.

Another definite distinction is to be found in the medullary rays of the two species. In *S. tuedianum*, as we have seen, the majority of the rays are multiseriate and vertically high, though uniseriate rays, sometimes of small height, also occur. In *S. tripartitum* a large proportion of the rays are uniseriate and many are quite low. This, though a difference of degree, gives quite a distinct character to the tangential sections of the wood.

For these reasons we are justified in recognising *S. tripartitum* as a distinct species of the genus.

Diagnosis of the two species

1. *Stenomyelon tuedianum*, Kidston.—Stem monostelic, primary xylem without xylem-parenchyma, divided more or less distinctly into three lobes by as many radiating and interrupted bands of parenchyma. Primary tracheides pitted on all walls. The protoxylems of the leaf-trace decurrent as exarch strands on the extremities of the lobes. Secondary thickening occurs. Secondary tracheides with bordered pits on radial walls only. Medullary rays numerous, one to six cells wide, usually high and multiseriate. Stele closely invested by a zone of sclerotic periderm or hard bast. Leaf-traces depart in rapid succession from the extremities of the lobes and repeatedly divide in the cortex. Leaf-trace protoxylems become immersed. Outer cortex of the “Sparganium” type.¹

2. *Stenomyelon tripartitum*, Kidston.—Primary xylem divided into three lobes, or, in small stems, continuous. Leaf-traces unknown, but apparently given off at long intervals. Protoxylem exarch, at the extremities of certain of the lobes. Medullary rays commonly uniseriate and often of small height. Cortex unknown.

It may be added that the primary xylem, in two of the known specimens, is considerably smaller than in any stem of *S. tuedianum* which has come under observation.

Affinities of Stenomyelon

In considering the affinities of the genus, the first question to be decided is whether the primary structure of the stem is to be interpreted as a protostele, or as a leaf-trace system. As Kidston and Gwynne-Vaughan point out, the leaf-traces depart from the stele in a perfectly protostelic manner, *i.e.* nothing of the nature

¹ This diagnosis is slightly modified from that given by Kidston and Gwynne-Vaughan, 1912, p. 270.

of a leaf-gap is left behind ; the trace is simply nipped off from a solid mass of xylem. The whole structure certainly suggests a protostele, for the primary xylem is nearly solid, and the narrow strips of parenchyma are not even continuous. The fact that in the smallest stem of *S. tripartitum* the primary xylem is quite undivided, materially strengthens this view. Apart from this, we might no doubt interpret the three lobes as a triplice of reparatory strands enclosing a narrow pith, and each lying immediately behind the leaf-trace which it gives off. This would make the whole essentially a leaf-trace system. But we have no analogy for such a system occupying practically the entire stele ; in all other cases it forms a peripheral zone, and appears to have been differentiated from the outer part only of the stele (Lyginopterideae and Calamopityeae). It thus seems most natural to adopt the protostelic hypothesis and to regard the intrastelar bands of parenchyma (when present) not as a pith, but as comparable rather to the network of cellular tissue in the primary wood of *Heterangium* or *Rhetinangium*, only in a simpler form.

On this view, *Stenomyelon* comes low down among the Pteridosperms, for the leaf-trace is only differentiated when it begins to pass out. Kidston and Gwynne-Vaughan, to whom our knowledge of the genus is primarily due, suggest no affinities, merely pointing out that it differs essentially from *Sutcliffia* (an aberrant genus of Medulloseae ; see p. 196), with which the exarch protoxylem suggested a comparison, in the absence of meristeles intervening between the stele and the leaf-traces. *Stenomyelon* is undoubtedly an isolated genus. The only, or at least the nearest, analogy seems to be with the Calamopityeae, with which it agrees in having numerous bundles in the petiole, all of which arise from the subdivision of a single original leaf-trace. There is no other group of Pteridosperms known for which this holds good. Another point of resemblance between the two families

is in the secondary thickening of the leaf-trace, persisting even after its first division. On the whole there seems to be more in common with *Calamopityeae* than with any other group, though there are great differences, for example, in the exarch xylem. The trace, however, as it passes outwards, becomes somewhat mesarch, and on the other hand there is some approach to exarchy in the protostelic species of *Calamopitys*, and probably more than an approach in the new species, *C. radiata* (p. 133).

If there is any real relation between the two families, the connection no doubt lay very far back; in some respects *Stenomyelon*, as we have interpreted its structure, is more primitive than any member of the *Calamopityeae*.

PROTOPITYEAE

Protopitys, Goeppert

Our knowledge of this group has hitherto been confined to the one species, *Protopitys Buchiana*, Goeppert, the commonest fossil in the Falkenberg beds, of Lower Carboniferous age. A similar plant has in more recent years been discovered in the Yoredale Rocks of Yorkshire, and will be referred to subsequently.

Protopitys Buchiana, Goeppert

This species has long been known; the secondary wood, which has a quite characteristic structure, was well described by Goeppert in 1850, and again by Kraus in 1887. The remarkable primary structure of the stem was first elucidated by Solms-Laubach, who published an admirable account of the fossil in 1893.

The stem attained a very large size. A specimen observed by Solms-Laubach was almost a foot and a half in diameter, though doubtless incomplete. Thus the plant became a tree, and as its leaves were ranged

in two opposite vertical rows, like the Traveller's Tree of Madagascar, it must have presented a strange appearance. The detailed structure has been chiefly investigated in a stem or branch of moderate dimensions, about 3.5 cm. in diameter, measured to the outside of the secondary wood.

The centre is occupied by an elliptical pith, which in this specimen is well over 1 cm. long by 4 mm. in

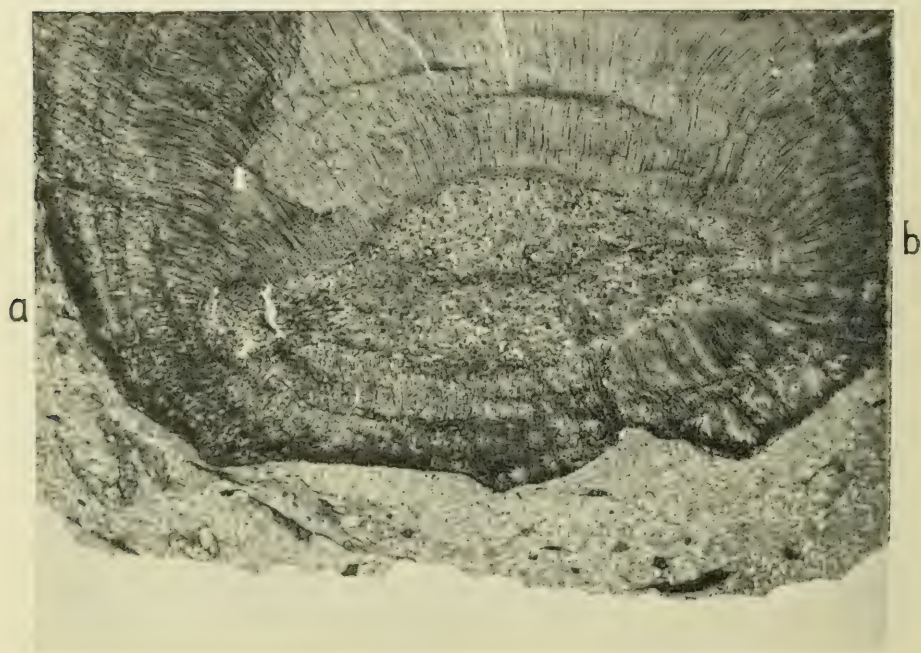


FIG. 59.—*Protopitys Buchiana*. Transverse section of stem, showing the pith and the primary, and part of the secondary wood. *a* and *b*, the ends shown enlarged in Figs. 60 and 61. \times about 6. 239a in Solms Coll. From a photograph by Mr. W. Tams.

maximum width, including the primary wood. The latter forms a continuous but very unequal zone, quite narrow at the sides, but swelling into a massive strand at each end of the elliptical transverse section (Fig. 59); these strands constitute the leaf-traces. The broad zone of secondary wood has a dense structure, resembling, as seen in transverse section, that of a Conifer. Some remains of the phloem and cortex are occasionally preserved.

The details of the primary structure, as shown in the transverse sections, vary according to the level at which the section is cut, for they are much affected by the successive emission and reparation of the large leaf-traces; we may take the section illustrated in Figs. 59-61 and in the diagram (Fig. 62, III.) as our starting-point.

The central tissue of the stele forms an extensive,

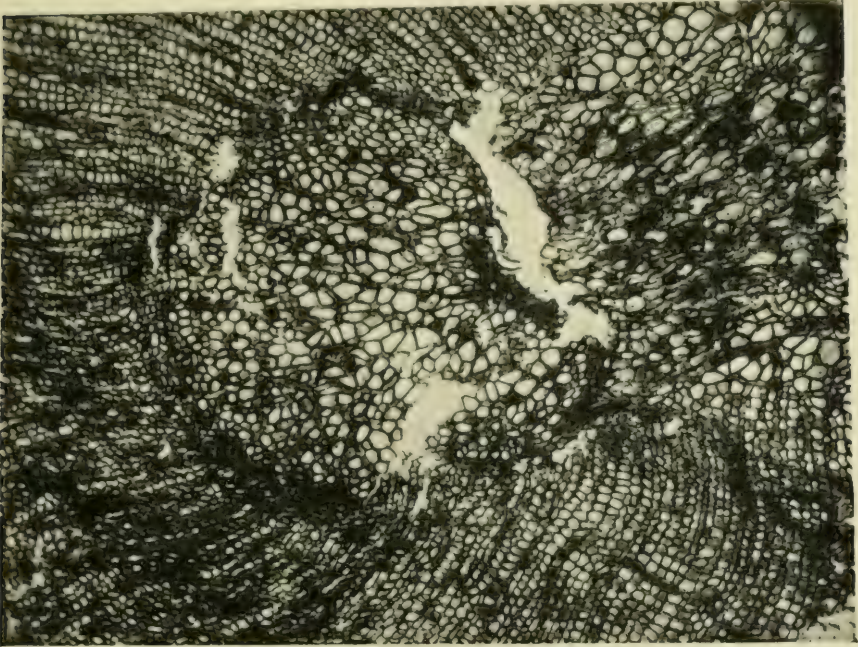


FIG. 60.—*Protopitys Buchiana*. Transverse section showing part of the primary wood and pith at the end *a*, in Fig. 59. The leaf-trace strand is just detaching itself from the lateral bands of xylem. The reparatory swellings of the xylem-bands are seen to the right of the trace. $\times 32$. From a photograph by Mr. W. Tams.

true pith, consisting of uniform, somewhat elongated cells, with no sign of medullary tracheides; some of the cells are distinguished by their dark contents. The primary xylem, as already mentioned, forms a practically continuous mantle round the pith. At the sides of the elliptical pith the mantle is quite thin, for the most part only from one to three tracheides in width. The primary tracheides are somewhat smaller than the pith-cells, but larger than the secondary elements abutting

on them externally; they thus constitute a fairly conspicuous band on either side (Fig. 59).

At each end of the ellipse we observe a massive xylem-strand, about 1.5 mm. in diameter. The position of the strands at the two ends is somewhat different. At the end marked *a* (Figs. 59, 60) the strand is just detached from the lateral xylem-bands, and is plunging into the secondary wood. It has a rounded section, flattened on the side towards the pith, and consists of rather large tracheides, intermixed with some xylem-parenchyma, often rendered more conspicuous by the dark contents of the cells (Fig. 60). There is no evident protoxylem at this level. This strand is the xylem of a leaf-trace, just preparing to pass out.

A little behind the leaf-trace, the xylem-band on either side is enlarged to form a marked projection about ten to twelve elements in depth (Fig. 60). These two prominences, like the large strand, contain a little xylem-parenchyma; the smallest tracheides, presumably constituting the protoxylem-groups, lie on the side towards the pith, indicating an *endarch* structure. These two projections represent, as we shall see, the reparatory strands of the leaf-trace (Fig. 59).

Turning now to the opposite end (*b*) (Fig. 59) of the elliptical pith, we again find a large xylem-strand, but of a somewhat different form, for it is concave, and has a slight indentation, on the face adjoining the pith (Fig. 61); it thus passes over somewhat gradually, on either side, into the narrow lateral xylem-bands, with which it is continuous. The general structure of the strand is similar to that previously described, but there is one important difference. Near the middle of the inner face and on either side of the median indentation, there are two definite groups of minute elements, no doubt the protoxylem (Fig. 61). Their position in this case is not *endarch* but *mesarch*, for they are separated from the pith by two or three layers of larger tracheides.

This xylem-strand is clearly a double one, though the fusion of its two constituent parts is nearly complete at the level shown. It represents a leaf-trace cut lower down in its course than that at *a*, already described.

By the comparison of different transverse sections, Solms-Laubach was able to explain the formation and course of the leaf-traces. Three distinct phases (though not a continuous series) are shown in the diagrams I.-III.

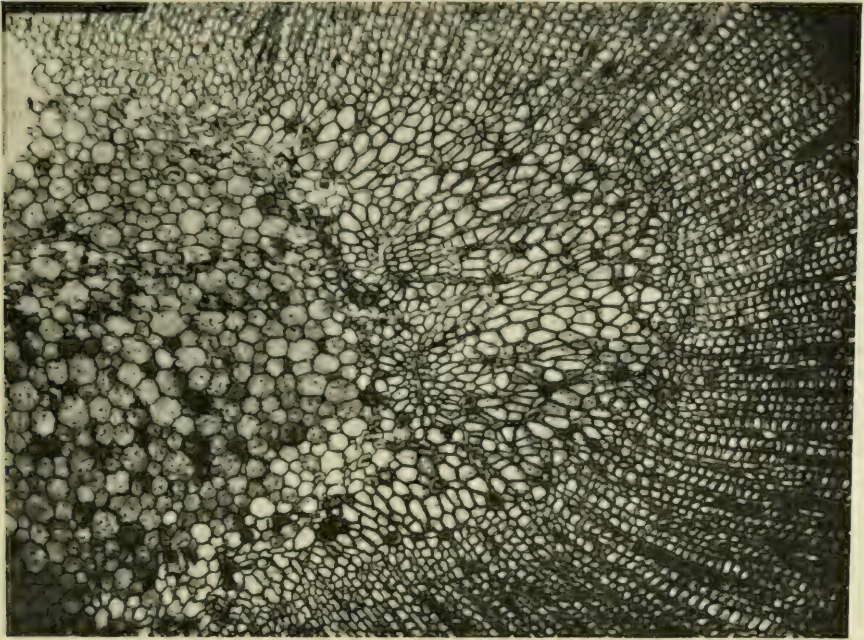


FIG. 61.—*Protopitys Buchiana*. Similar section at the end *b* in Fig. 59, showing a leaf-trace strand lower down in its course. It is here continuous with the xylem-bands and has two immersed protoxylem-groups. $\times 32$. From a photograph by Mr. W. Tams.

(Fig. 62), the last of the three being identical with the section already described and figured in detail. This figure will therefore be readily understood. In all the diagrams the dark points indicate the approximate position of the protoxylem-groups. It will be observed that in Diagram III. none are shown in the trace at *a*, which is beginning to pass out. Behind this trace the two lateral reparatory strands or prominences, with their protoxylem points, are evident. At the end *b*, the com-

position of the new trace from the two united reparatory strands is indicated.

In Diagram II. trace *a* is shown at a level intermediate between *a* and *b* in the section just described; it has lost its protoxylem, but has not yet detached itself from the xylem-mantle; the reparatory strands, which will appear behind it, are not yet differentiated. At the

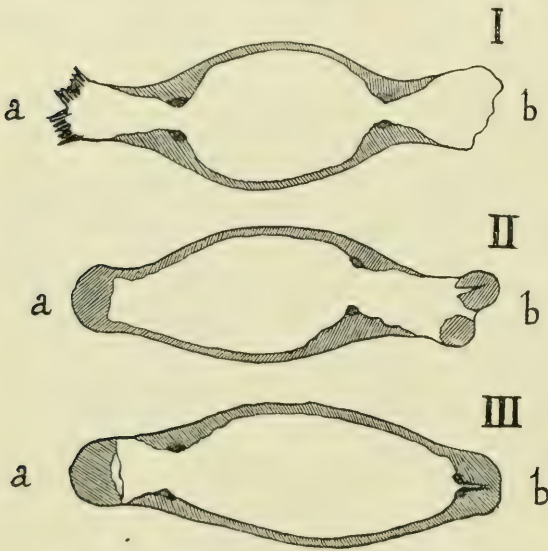


FIG. 62.—*Protopitys Buchiana*. Three diagrams of transverse sections of the primary wood, to show emission of leaf-traces. I. At *a* the double trace is passing out, at *b* it has already gone. Reparatory swellings conspicuous at both ends. II. At *a* the trace is undivided and not yet detached. At *b* it is detached and divided into two. Reparatory swellings only developed at *b* end. III. At *a* the trace is detached, though not yet divided. At *b* it is cut low down in its course. Reparatory swellings only formed at *a* end. This is the section shown in Figs. 59-61. The black spots indicate protoxylem throughout. After Solms-Laubach.

end *b*, the leaf-trace is intersected high up in its course; it is quite detached from the xylem-mantle and has already divided into two strands, which have no protoxylem. The two reparatory strands which will replace the outgoing trace are already prominent.

Diagram I. shows a different phase again, for it passes above the point of exit of both leaf-traces. The trace at *a* is still visible,

but cut obliquely; it is forking to form two strands. The reparatory projections behind it are about to meet. At the end *b* the trace has disappeared altogether, leaving the pith open. Here also the reparatory strands are very prominent.

It will be noticed that the two traces are never shown in the same phase in any one section, for they were given off alternately, the arrangement of the traces, and there-

fore of the leaves which they supplied, thus being distichous. Solms-Laubach obtained direct evidence of this by means of a longitudinal section in the plane of the major axis of the pith. It shows clearly how the three traces met with were given off alternately on opposite sides, each leaving a gap just above its exit.

This is the first example we have met with of a distichous phyllotaxis ; so far, it stands alone among plants referred to Pteridosperms, though instances are well known among fossil Tree-ferns (*Megaphyton*).

The mode of formation of the leaf-trace is also exceptional. We may sum up the process as follows : When the previous trace has passed out, the parts of the xylem-mantle near the edges of the gap become thickened, forming two opposite prominences ; they then meet and fuse into a solid strand to form the new leaf-trace, which now detaches itself from the xylem-mantle and divides into two as it moves outwards. The construction of the trace by the fusion of two reparatory strands is quite peculiar ; somewhat similar thickenings of the edges of the leaf-gap have been observed in some recent Ferns with a tubular stele, but the analogy seems remote. As Solms-Laubach points out, the reparatory structures are not properly described as "strands," for they are merely enlarged portions of a continuous xylem-ring, and only become free when the new trace is constituted.

The behaviour of the protoxylem is also remarkable. Endarch in the reparatory strands, it becomes mesarch in the fused leaf-trace, owing probably to the mode of fusion, and then dies out altogether. The change from endarch to mesarch structure has a parallel in the xylem-strands of the *Eristophyton* sub-genus of *Calamopitys*, with which there is otherwise no analogy.

In the primary xylem, so far as Solms-Laubach observed, the tracheides are typically scalariform ; no pitted elements are recorded. This again is an exceptional feature. The secondary wood is equally peculiar

and unlike that of any plant we have previously described. In transverse section, as already mentioned, it has the dense appearance of a Coniferous or Cordaitan wood (Fig. 59); its special characters appear in the radial and tangential aspects. The pits, limited as usual to the radial walls, are transversely elongated, and for the most part form a single vertical series; occasionally the row is double and the pits shorter. The structure is almost intermediate between the scalariform and the ordinary pitted types. Where the preservation is exceptionally good, it can be seen that the pits are bordered, with slits inclined, as usual, in opposite directions on adjacent walls.

Prof. Seward has pointed out that a somewhat similar form of pitting occurs in a Mesozoic Conifer, *Xenoxylon phyllocladoides*.¹

The medullary rays are narrow and for the most part of extremely small height; in fact, as often as not, they are only one cell high, thus forming a single radial line of cells. The greatest height observed was sixteen cells, but this is quite exceptional. The rays are as a rule uniseriate, but sometimes two, or very rarely three cells wide in the middle. The general character of the wood is thus quite peculiar and different from that of the great majority of Pteridosperms.

In one case Solms-Laubach was able to examine the structure of the phloem, which is seldom preserved. He found that it consists of alternating concentric zones of hard and soft bast; the former has an unusual character, for it consists of short stone-cells, and no medullary rays can be distinguished. A comparison with the corresponding region of *Stenomyelon tuedianum* was suggested above (p. 138). The zones of soft bast contain long tubular elements, presumably the sieve-tubes.

Some fragments of tissue associated with the stem

¹ Seward *Fossil Plants*, vol. iii. 1917, p. 213.

seem to belong to the lamina of a leaf, rather than to the cortex, for an apparent epidermis is present on both sides ; the tissue is badly preserved, but small vascular bundles, with scalariform tracheides, can be recognised.

Solms-Laubach observed the base of a branch in connection with the main stem. The stele of the branch has the same structure as that of the parent axis, on which it is inserted obliquely. The size of the pith diminishes, and the amount of primary xylem increases, as the branch-stele is followed inwards to its junction with the main axis.¹

Protopitys radicans, Kidston

This species is derived from the Yoredale rocks of Swarth Fell, Yorkshire, and thus belongs to the upper part of the Lower Carboniferous. Our knowledge of the plant is due to Dr. Kidston, who still has the specimens under investigation. The characters of the secondary wood, namely the pitting of the tracheides and the structure of the medullary rays, indicate the reference of the species to *Protopitys*. The cortex is preserved and is traversed by a zone of embedded roots, a peculiar feature, which suggested the specific name. Pending further investigation especially of the primary tissues, we can only record the occurrence of the species, which promises to be of much interest.

Affinities of Protopityeae

Protopitys seems to be the most isolated of the genera which are referred, on anatomical grounds, to the Pteridosperms or Cycadofilices. Its peculiarities have been

¹ See Solms-Laubach, "Über die in den Kalksteinen des Kulms von Glätzisch-Falkenberg in Schlesien enthaltenen structurbiotenden Pflanzenreste," ii. *Bot. Zeitung*, Band li. 1893, p. 197. The older references are given in this paper.

pointed out in the course of the description of *P. Buchiana*, but may be shortly recapitulated as follows :

1. The distichous phyllotaxis.
2. The continuous, but unequal ring of primary xylem.
3. The union of two reparatory masses to form the leaf-trace.
4. The endarch structure in the reparatory region, becoming mesarch in the leaf-trace, in which, however, the protoxylem is soon lost.
5. The scalariform tracheides of the primary xylem.
6. The semi-scalariform pitting of the secondary wood.
7. The narrow and usually very low medullary rays.

The distichous phyllotaxis appears to be only paralleled, among Palaeozoic plants, in the Fern *Megaphytum*, which has otherwise nothing in common with our fossil. The unequal xylem-ring may find a partial analogy in certain species of *Calamopityx* and *Lyginopteris*, but the vascular system is so different in the two cases that no real resemblance can be traced.

The fusion of two equivalent reparatory units to form the new leaf-trace, and their origin as swellings on the xylem-ring, seem to be quite peculiar features ; the thickenings on the edge of the leaf-gap in some solenostelic Ferns are not comparable, for they are cauline in nature, and are not concerned in the formation of the leaf-trace.¹

The change from endarch to mesarch structure in the ascending leaf-trace is of course familiar (e.g. *Calamopityx*, sub-genus *Eristophyton*, *Biligneæ*, *Mesoxylon*), but the dying out of the protoxylem in the upward direction seems to be without analogy, while the reverse is often the case.

The scalariform sculpturing of the tracheides of the

¹ D. T. Gwynne-Vaughan, "Observations on the anatomy of solenostelic Ferns," Part ii., *Ann. of Bot.* vol. xvii. 1903, pp. 692, 698.

primary wood, while pitted elements are absent, is an unusual feature in the stem of Pteridosperms; analogies among higher plants, such as the Cordaiteae, are too remote to be significant. The nearest parallel is with the primary xylem of the Cladoxyleae, another isolated group, to be described in the next section.

The wood of *Protopitys*, in fact, is altogether peculiar, for the secondary elements constantly show scalariform or semi-scalariform pitting, very different from the usual round, multi-seriate pits of other families. Here, also, the Cladoxyleae present the closest analogies (see below, p. 160).

The medullary rays of *Protopitys* are remarkable for being, as a rule, uniseriate, with a large proportion of "one-storied" rays, *i.e.* rays only one cell high. These little rays are often strung together in moniliform rows. Some similarity is shown here also by the secondary wood of Cladoxyleae, in which the rays are usually uniseriate and often one-storied.

The general result of our brief survey is to confirm the impression that *Protopitys* is an isolated type; there is, in fact, no agreement of a really suggestive kind with any other group, except, perhaps the highly problematic Cladoxyleae, with which the structure of the wood shows a close analogy, though the general organisation is totally different.

All the families previously considered have shown a certain relationship, sufficient to justify us in classing them as Pteridosperms, though it is only in the Lyginopterideae that we know the seeds. With the Protopityeae the case is different, the type stands apart, and we include it under the heading Pteridosperms or Cycadofilices, because it is in some ways Fern-like, but is not a Fern. Solms-Laubach, to whom we owe our knowledge of the true structure of the plant, put *Protopitys* with *Lyginopteris* and *Heterangium*, among plants which are intermediate in their characters between Filicineae and

Gymnosperms and may represent descendants in different directions of a primitive group common to both.¹

This was in 1893, when comparatively few such plants were known. Solms first made *Protopitys* into a distinct family, and pointed out the absence of any Cycad-like features, such as are found in *Lyginopteris*. Since that time, in spite of many new discoveries, there has been little to connect *Protopitys* any more closely with the other families now grouped under Pteridosperms.

THE CLADOXYLEAE

We now come to an interesting group of early Palaeozoic plants, very different from any of those already described and, in fact, remarkably isolated, so that its affinities are open to much doubt. The Cladoxyleae have been known for a long time; a number of forms were described by Unger in 1856; his specimens came from Saalfeld in Thuringen, the same locality which yielded *Calamopitys Saturni*, *C. annularis*, *Clepsydropsis antiqua* and a number of other fossils of interest. Our knowledge of the family was first placed on a scientific basis by Solms-Laubach forty years after the date of Unger's discoveries; in recent years the investigation has been taken up anew by Prof. P. Bertrand, whose results are not yet published in full.

The stems referred to this family agree in the fact that they all have a complex, polystelic structure, thus differing completely from the families of "Pteridosperms" already described, in which the vascular system of the stem is always referable to a single central cylinder. In the Cladoxyleae there is the further peculiarity that in mature specimens each stele has its own secondary zone of tissue, though in other cases the primary structure has remained unaltered, thus presenting the general appearance of a polystelic Fern-stem (cf. Figs. 63 and

¹ Solms, *l.c.* 1893, p. 207.

64). The petioles have now been recognised in some cases, but we are still practically without information as to the external habit, while the fructification is wholly unknown.

Dr. Bertrand recognises three genera in the family :



FIG. 63.—*Cladoxylon taeniatum*. Transverse section of stem, showing the numerous steles, those of the outer zone radially elongated and those of the centre circular. The three steles at the top of the figure are believed to be destined for a leaf-trace. \times about 3. From a photograph by Dr. Bertrand.

Cladoxylon, Unger, *Völkelia*, Solms, and *Steloxylon*, Solms ; the last mentioned, however, is still a highly problematic fossil. *Cladoxylon* and *Völkelia* are of Lower Carboniferous or possibly, as regards the Thuringian species, of Upper Devonian age ; the horizon to which *Steloxylon*

belongs is open to question. We will begin with the type genus *Cladoxylon*.¹

Cladoxylon, Unger

This is the best-known genus of the family. Unger described no less than eight species, and referred them to five different genera; we may now, however, provisionally adopt the simple view of Dr. Bertrand, who assigns Unger's forms to the one genus, with three Saalfeld species, *C. mirabile*, Unger, *C. taeniatum* (Unger), and *C. Solmsi*, P.B. To these we must add the Scottish species *C. Kidstoni*, discovered by Dr. Kidston and described by Solms-Laubach in 1910.

The larger specimens, reaching 4 cm. or more in diameter, have the typical *Cladoxylon* features and were no doubt, the stems; others, usually smaller, and with a somewhat different, though still polystelic structure, have now been identified as the petiole or rachis. Taking the stem first, we find the following characters common to the genus. The numerous steles are for the most part elongated in a radial direction, an unusual feature in polystelic plants (Figs. 63, 64). Each stele has a median band or mass of primary wood, in which the tracheides are irregularly arranged; at the distal end, or about the middle if the stele is cylindrical, there is a gap or loop containing the protoxylem elements. Usually, but not always, the primary xylem is surrounded completely or incompletely, as the case may be, by a zone of radially seriated, secondary wood, traversed by uniseriate, medullary rays. The pitting is

¹ See Unger, in Richter and Unger, "Beitrag zur Paläontologie des Thüringer Waldes," 2ter Theil, *Denkschriften der K. Akad. d. Wiss., Wien*, Band xi. 1856; Solms-Laubach, "Über die seinerzeit von Unger beschriebenen strukturbietenden Pflanzenreste, etc." *Abhandl. d. K. Preuss. Geol. Landesanstalt*, 23, 1896; P. Bertrand, "État actuel de nos connaissances sur les genres *Cladoxylon* et *Steloxylon*," *Assoc. Franç. pour l'Avancement des Sciences*, Congrès de Havre, 1914, p. 446.

generally scalariform, that of the secondary elements being limited in all probability to the radial walls. Externally the wood of each stele is enclosed in a layer of phloem, usually ill-preserved. The surrounding tissue is parenchymatous, but in the parts remote from the steles a fibrous structure has been observed.

The two principal Saalfeld types are *C. mirabile* and *C. taeniatum*. In *C. mirabile* the steles, as seen in transverse section, are usually long and often forked or curved, sometimes assuming a U form, with the concavity directed outwards (Fig. 64). Where a curved stele abuts with both ends on the periphery, each arm has its own peripheral loop or protoxylem group. The steles in their longitudinal course occasionally fused with one another. The secondary thickening is not usually very pronounced; sometimes it is only present on one side of the stele, while in other cases it is absent altogether, as in the stem shown in Fig. 64. Such stems, no doubt representing the young condition, were in some cases separated by Unger under the name *Arctopodium radiatum*.

The second type, *Cladoxylon taeniatum*, is characterised by the usually straight steles; those of the outer zone are radially directed and may be much elongated or elliptical in section, the longer and shorter steles irregularly alternating. There is also a central group of steles (five in number in the case figured) which are more or less circular in section. Similar round central steles ("star-rings") occur in several of the Medulloseae, another polystelic family, to be described in the next chapter. In *C. taeniatum* there is a great development of secondary tissues around each stele, as shown in Fig. 63.¹

The third species, *C. Solmsi*, P.B., resembles *C. taeniatum*, but without the central steles, while the occasional curvature of the steles recalls *C. mirabile*;

¹ *C. dubium*, Unger, often mentioned in the literature, seems to be a form of *C. taeniatum* with shorter steles.

this is the plant in which the petiole was first recognised by Solms-Laubach.¹

The secondary wood seems to be very uniform throughout the genus; in some cases it is most developed on the side of the steles directed towards the centre of the stem, a peculiarity which recurs in some species of *Medullosa* (see p. 176).

The narrow medullary rays are characteristic—they are often only one cell high as well as one cell wide, thus being reduced to a single radial row of cells.

As already mentioned, there is one British fossil which has been placed in the genus *Cladoxylon*. The specimen, discovered by Dr. Kidston, is of Lower Carboniferous age and is derived from the Calceiferous Sandstone Series of Berwickshire. It was described and figured by Solms-Laubach, who named it *C. Kidstoni*.²

The species is a fragment of a rather large stem, containing part of a ring of steles, ovate in transverse section and but little elongated in the radial direction (Fig. 67, A). In each there is a narrow band of primary wood, surrounded by a broad secondary zone chiefly developed on the side presumably facing the centre of the stem, while on the opposite side it is limited to one or two small wedges.

The pitting of the secondary tracheides is confined to the radial walls. Prof. Seward, who has re-investigated the specimen, finds that the pits are either “uniseriate and transversely elongated, very like those of *Protopitys*, or biseriate and almost circular, like those of Conifers.” Sometimes there are three rows.³

¹ *L.c.* 1896, p. 55, Taf. ii. Fig. 13, Taf. iii. Fig. 4. Solms called this specimen “*C. mirabile?*” He also figured and described a probable petiole in a specimen which he named *Arctopodium radiatum* (see our Fig. 64).

² Solms-Laubach, “Über die in den Kalksteinen von Glätzisch-Falkenberg in Schlesien erhaltenen structurbiotenden Pflanzenreste,” iv., *Zeitschrift für Botanik*, ii. 1910, p. 537, Figs. 5, 7, 11, 13.

³ Seward, *Fossil Plants*, vol. iii. pp. 205-207, Fig. 460, A, C, 1917.

The numerous medullary rays are almost always uniseriate ; the tangential section of the wood is a good deal like that of *Protopitys*. The presence of rays favours the reference of the plant to *Cladoxylon*, rather than the next genus *Völkelia*, to which it otherwise bears some resemblance (Fig. 67, A and B). Prof. Seward does not accept the evidence for the attribution to *Cladoxylon* as convincing, but no other affinities have been suggested, beyond a certain analogy with the problematic South African genus *Rhexoxylon* (see p. 228).

We now come to the question of the petiole and leaf-trace of *Cladoxylon*. As already mentioned, the base of a petiole was observed by Solms-Laubach in the form named by Dr. Bertrand *C. Solmsi*, and also in a specimen described under Unger's name *Arctopodium radiatum*. The latter case is shown in Fig. 64 from a photograph by Dr. Bertrand, to whom our present knowledge of the appendages of *Cladoxylon* is due.¹

The specimen shown in Fig. 64 is very clear. The stem is of the *C. mirabile* type, but without secondary thickening, *i.e.* it was still young, which no doubt accounts for the petiole still being attached to it ; the two organs are connected by parenchyma, though at this level the vascular systems are already separated. The petiole contains eight vascular strands, one of which seems to be dividing. They are round or elliptical in section, and quite different in form from the steles of the stem. Each strand has a well-marked median band or group of protoxylem. As might be expected, all the wood appears to be primary. The ground-tissue is also well preserved, and on the abaxial surface there is a layer resembling a hairy covering.

The bodies, roundish in section, which accompany the petiole are described by Dr. Bertrand as apherblae,

¹ I am indebted to Dr. Bertrand for valuable information given in correspondence, in addition to his preliminary notes already published.

each containing a single bundle, or sometimes two, resembling those of the petiole. The aphlebiae were finely divided.

The emission of the leaf-trace has been studied by Dr. Bertrand ; an example is shown in Fig. 65, a diagram



FIG. 64.—*Arctopodium radiatum*, probably a young stem of *Cladoxylon mirabile*. Below, the stem is shown, with the curved and forked steles, without secondary thickening. Connected with the stem above is a petiole containing several elliptical bundles. The roundish structures on either side are the aphlebiae. \times about 7. From a photograph by Dr. P. Bertrand.

taken from one of Unger's sections now in the Jermyn Street Museum. The typical process is described as follows:—The outgoing mass is formed at the expense of four to six radiating plates of the stem. The four median plates each give off two outgoing rings ; the end

plates only one each ; the latter pass out into the finely-divided aphlebiae. The eight remaining rings arrange themselves in a circle, first becoming flattened tangentially, and then elongating radially. They have not been followed out into the petiole, but comparison suggests that the latter organ assumes the structure of *Hierogramma*.

The latter is one of Unger's genera, which, as now suggested, consists of the petioles of Cladoxylon. An

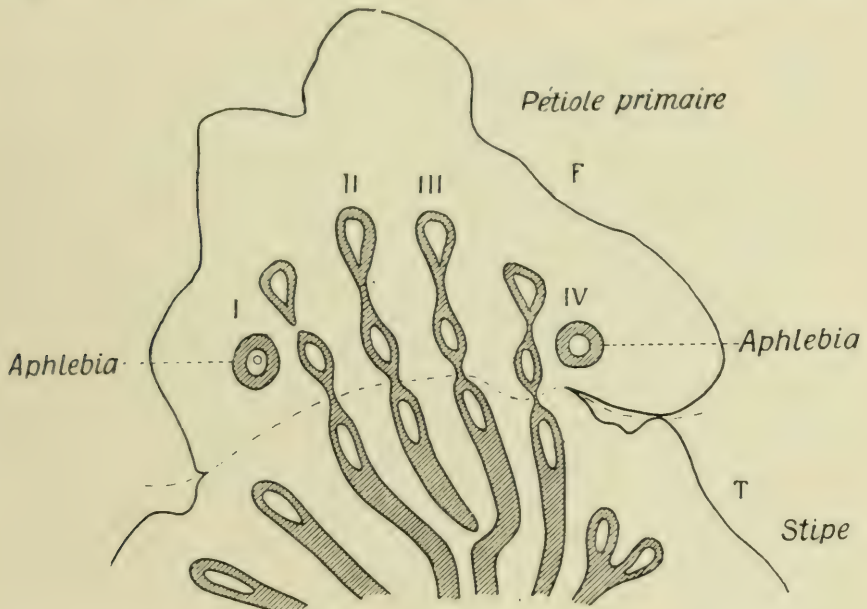


FIG. 65.—Diagram of stem in transverse section, to show the emission of a leaf-trace entering a petiole. *T*, stem; *F*, base of petiole; *I*, *IV*, bundles destined for aphlebiae; *II*, *III*, central strands of leaf-trace. Jermyn Street Coll., 15871. After Dr. P. Bertrand.

example of *Hierogramma mysticum* is shown in Fig. 66 ; the great tangential elongation of the outer steles is an indication of approaching dichotomy. A bilateral symmetry is characteristic of these organs and serves to distinguish them from the stems. The picturesque name given by Unger indicates the hieroglyphic-like pattern of the transverse section.

It will be seen that the structure of *Hierogramma* is very different from that of the attached petiole shown in Fig. 64. The latter, however, is cut near the base,

and the structure may have changed higher up; it is possible, as Dr. Bertrand has suggested, that *Hierogramma* may have been the petiole of the species *C. taeniatum*. In the leaf-base found by Solms-Laubach in connection with the stem now named *Cladoxylon Solmsi*, the single bundle shown resembles that of a *Hierogramma*.

Syncardia, another of Unger's genera, is described by Dr. Bertrand as a reduced state of *Hierogramma* with from four to six xylem plates. Probably it represents

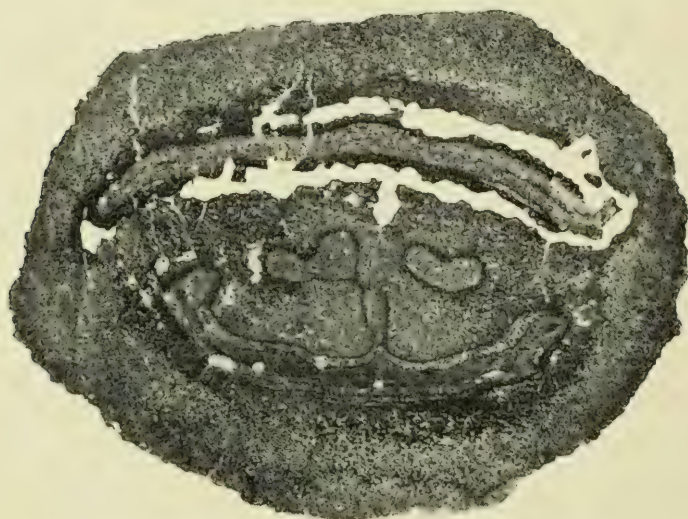


FIG. 66.—*Hierogramma mysticum* (petiole of a *Cladoxylon*). Transverse section, showing the stellate system of a petiole about to dichotomise. $\times 8$. From a photograph by Dr. P. Bertrand.

a secondary rachis of the same leaf, but the connection has not been observed.

From the arrangement of the leaf-traces in *C. mirabile* (*Arctopodium radiatum*) Dr. Bertrand finds that the phyllotaxis was spiral and the divergence probably $\frac{2}{5}$.

It will be seen that our knowledge of the genus *Cladoxylon* is still very incomplete, and that various points need corroboration. We may hope for further light from the extension of the important investigations which Dr. Bertrand has initiated.¹

¹ See, in addition to the paper above cited, P. Bertrand, "Observations sur les Cladoxylées," *Comptes Rendus de l'Association Franç. pour*

VÖLKELIA, Solms

This genus was founded by Solms-Laubach in 1910 on the *Sphenopteris refracta* of Göppert. The specimens are derived from the Lower Carboniferous of Falkenberg in Silesia.¹ The plant was put in *Sphenopteris* by its discoverer because some of the fragments include portions of a compound frond, bearing finely divided leaflets. But, as Solms-Laubach has pointed out, the fragments showing the foliage do not show structure, and *vice versa*. Hence there is no actual proof that the two kinds of specimens belonged to the same plant, though there is a certain probability that this may have been the case. If it were so, this would be the only instance in which we have any indication of the outward habit of a member of the Cladoxyleae.

The stem, about 8-10 mm. in diameter, has the highly polystelic structure usual in the family. In fact, the general appearance of the transverse section is almost identical with that of the *Cladoxylon dubium* of Unger, who actually referred Göppert's specimens to that species. In *Völkelia* there are a dozen or more ovate or angular steles, large and small; the larger steles nearly meet at the centre, while the smaller ones are wedged in between them, towards the periphery (Fig. 67, B). The main part of each stele is formed of large, radially arranged scalariform tracheides, the inner layers of which have often collapsed. This secondary zone is thickest towards the centre of the stem, and sometimes

l'Avancement des Sciences, Congrès de Dijon, 1911; "L'Étude du stipe de *l'Asteropteris noveboracensis*," XII. Session du Congrès géologique international, Ottawa, 1913. The latter paper contains diagrams of the leaf-traces of *Cladoxylon*. The note of 1911 was written at a time when the author thought that *Clepsydropsis* might be the petiole of *Cladoxylon*, a view which he has since abandoned, having recognised the true petioles belonging to the genus, as stated in the text.

¹ See Solms-Laubach, 1910, above cited, and the earlier works there referred to.

almost dies out on the peripheral side of the stele. In the interior, eccentrically placed towards the peripheral end, there is a well-preserved primary strand of smaller elements. In this group the outer tracheides, like those of the secondary wood, are scalariform, but about the centre narrow, annular, and reticulate tracheides are intermingled with long-celled parenchyma. This, then, is the seat of the protoxylem.

The characteristic feature of *Völkelia* lies in the structure of the secondary wood; the tracheides are pitted on all their walls, and there is no trace of any medullary rays. So simple a structure of a secondary zone of xylem is rarely met with, and at once distinguishes the genus from its allies.

The steles are only slightly elongated (as seen in transverse section) in the radial direction; the phloem is not preserved; the outer zone of the cortex has a fibrous character, and approaches the *Dictyoxylon* type.

Thus *Völkelia* in its general construction betrays an evident affinity with *Cladoxylon*, and can only be placed in the same family; in the structure of the wood it is quite peculiar, and simpler than any other plant referred to the Pteridosperms or Cycadofilices.

According to the views of Dr. Bertrand, *Steloxylon* should be included in the Cladoxyleae, but in the present state of our knowledge it will be more convenient to take that doubtful genus after we have dealt with the Medulloseae.

Affinities of the Cladoxyleae

It is sufficiently plain, from what has been said above, that this family is a very isolated one and shows no evident affinity with any of those previously described. Certain points in common with *Protopitys* in the structure of the wood have already been pointed out; the general structure, however, is so totally different that no near relationship can be imagined. In the next chapter we

shall make ourselves acquainted with an important group, the Medulloseae, which, like the Cladoxyleae,

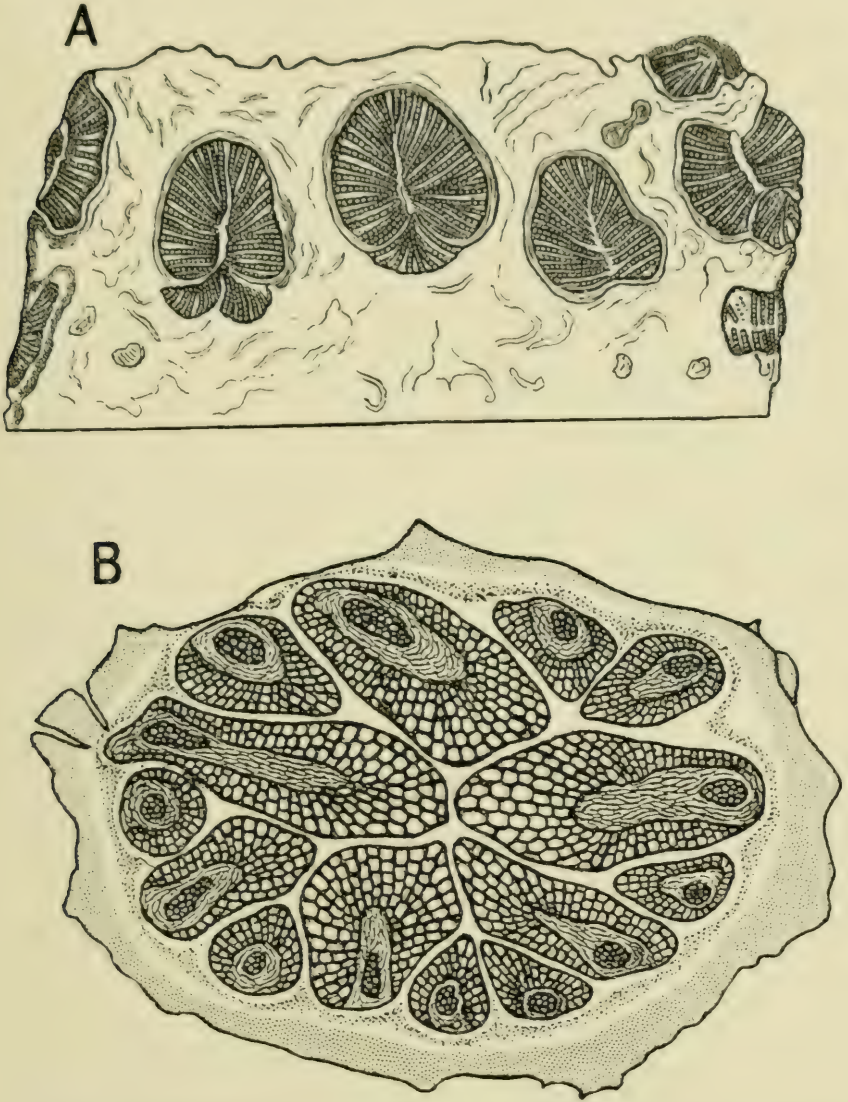


FIG. 67.—A. *Cladoxylon Kidstoni*. Transverse section, showing several steles, with very unequal secondary thickening. Slightly magnified. After Solms-Laubach. B. *Völkelia refracta*. Transverse section of stem, somewhat diagrammatic, showing the numerous steles. In each the primary wood is near the periphery. Inner layers of secondary wood collapsed—outer layers preserved. \times about 6. After Solms-Laubach, modified.

combine polystely with secondary growth. But here too there are difficulties in the way of assuming a real affinity.

The radially orientated steles, the peripheral loops, the usually scalariform tracheides, the participation of several steles in constituting the leaf-trace, the peculiar stem-like structure of the petiole and the presence of aphlebiae seem to be the chief characters of the Cladoxyleae.

How are we to class them? Dr. Bertrand in his note of 1914 says that they appear to constitute a new group of ancient Phanerogams. More recently, in a letter dated August 3, 1920, he expresses the view that the Cladoxyleae are very primitive types, and that it is necessary to make them a class apart—one cannot class them with complete certainty either among the Ferns or among the Phanerogams, yet they surely belonged to one or other of these two groups and *very probably* to the Phanerogams. He points out that in them the distinction between the stems and the petioles was still very slightly marked.

This discloses a very interesting position. We appear to have in the Cladoxyleae a very primitive group, with little differentiation between axis and appendages, and yet there is a probability that they were already Phanerogams (*i.e.* Pteridosperms in a wide sense). Dr. Bertrand's remarks suggest the belief, which seems to be growing stronger every day, that the Spermatophyta may go back as far as any of the recognised types of Pteridophyta, and may have had their origin among quite early vascular plants, on a level, perhaps, with the Psilophytales.

At the same time it must be recognised that the evidence for referring the Cladoxyleae to Pteridosperms is extremely indirect. As Dr. Bertrand remarks, the only other group with which they can be compared is the Ferns; they have something in common with the latter, especially with the Zgyopterideae, in the peripheral loops of the xylem and in the aphlebiae.¹

¹ Aphlebiae, however, appear to occur also on certain fronds referred to Pteridosperms.

In other respects, especially the complex vascular system of the petiole, the organisation is very different from anything we find among Palaeozoic Ferns; the analogies with some of the Pteridosperms, though still remote, are somewhat closer. On the whole, therefore, the opinion cautiously expressed by Dr. Bertrand, in essential agreement with that of Solms-Laubach, appears to be justified.

CHAPTER III

PTERIDOSPERMEAE—continued

Medulloseae ; *Aneimiteae* ; *Seed-bearing Pecopterideae* ;
Dolerophyllum ; *Steloxylon* ; *Rhexoxylon* ; *Cycad-*
oxyleae ; *Summary*

MEDULLOSEAE

HABIT.—As long ago as 1883 the Austrian palaeobotanist Stur, as already mentioned, proposed to exclude certain of the principal genera of fossil Fern-like fronds from the Ferns, on the ground that, in spite of all the research devoted to them, they had never been found to bear Filicinean fructifications. The genera which he specially cited were *Neuropteris*, *Alethopteris*,¹ *Odontopteris*, and *Dictyopteris* ; these genera, along with others, are now

¹ In a new species referred to *Alethopteris*, *A. Pfeilstickeri*, from the Coal-measures of Saxony, Prof. R. Beck recently described a supposed Fern-like fructification. It consists of numerous round pustules, interpreted as sori, arranged in rows on the lower side of certain leaflets. The pustules lie *between* the veins and not over them, a position which is unfavourable to the interpretation of these bodies as sori. The supposed indications of sporangia appear to be of doubtful value. See R. Beck, "*Alethopteris Pfeilstickeri*, ein neuer Farn aus dem Oberkarbon von Lugau-Ölsnitz," *Abhandl. d. naturwiss. Gesellschaft ISIS in Dresden*, 1917, p. 23. For a criticism see W. Gothan, "Paläobotanische Veröffentlichungen aus den Jahren 1914-1918," *Zeitschrift für Botanik*, Band II, 1919, p. 192. The Abbé Carpentier has recently found some scattered pollen-grains in cavities formed in the leaflets of *Alethopteris Grandini*. There seems, however, to be no proof that the pollen-grains are *in situ*. Carpentier, "Note sur quelques Végétaux à structure conservée," etc., *Revue gén. de Botanique*, t. xxxiii. p. 684, 1921.

often grouped in the family Neuropterideae, based on external characters, corresponding in part, if not altogether, to the Medulloseae as defined by structure. Recent investigation has fully justified Stur's conclusion (though not accepted at the time), and, as we shall see, there is now every reason to believe that the Neuropterideae generally were seed-bearing plants (Pterido-



FIG. 68.—*Neuropteris heterophylla*. Part of vegetative frond, slightly enlarged.
From a photograph by Dr. R. Kidston, F.R.S.

sperms) and not Ferns. Among the genera in question *Neuropteris* and *Alethopteris* are the most extensive and, at present, the best investigated.

The leaves of *Neuropteris* are of a very large size, bipinnate, tripinnate, or even quadripinnate in composition, with ovate or oblong leaflets somewhat cordate at the base, and usually attached to the rachis by a short stalk. The median nerve of the pinnule is distinct till near the end, where it breaks up into smaller dichotomous

nervules ; similar nervules are given off from the sides of the median nerve throughout its length ; they leave the latter at an acute angle, and bend outwards to the margin (Fig. 68). The fronds recall those of some recent *Osmundas*.

In some cases, pinnae of a different form, without a median nerve, and described under the name of *Cyclopteris*, were attached directly to the rachis, and may have been of a stipellar nature. These organs are of the same kind as the "aphlebiae" mentioned in Vol. I., Chapters VIII. and IX., as occurring on the fronds of Ferns.

In the genus *Alethopteris* the leaves are likewise large, and bi- to tripinnate, but here the thick, usually oblong pinnules are inserted on the rachis by a broad, decurrent base, and are in some cases confluent with one another. The edges of each leaflet are incurved on the lower side. The median nerve

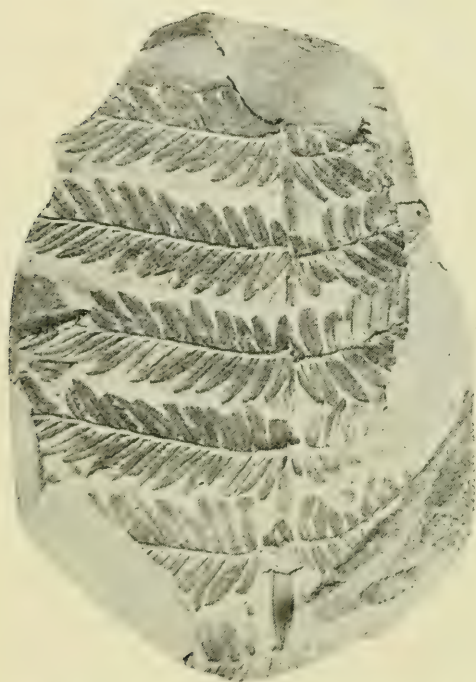


FIG. 69.—*Alethopteris lonchitica* (foliage of a *Medullosa*). Part of frond. Reduced. From a photograph by Mr. W. Hemingway.

extends the whole length of the pinnule, and is prominent on its under surface ; the secondary nerves leave the median one at a wide angle, and pass directly, with or without dichotomy, to the margin (see Fig. 69). The habit resembles that of the recent Marattiaceous Fern *Angiopteris*.

In the case of both these so-called genera, founded on the external characters of the leaf, there is now good evidence that they belonged to stems of the family

Medulloseae, of which the structural characters are known. The nature of the proof will be given later, after describing the anatomy of the stem; but, while considering this, it is necessary to bear in mind that we are dealing with plants which possessed a highly compound Fern-like foliage, and which, in some forms at any rate, must have had a habit not unlike that of some of the existing Tree-ferns. We will first describe the anatomy of various representatives of the family, beginning with the type genus *Medullosa*, and will then go on to the evidence which we now possess as to the reproductive organs, especially the seeds.

ANATOMY—*Medullosa*.—The anatomical description will be based, in the first instance, on a British species, which is of greater geological antiquity than most other known members of the genus, and is likewise simpler in structure. As this form is now known with a considerable degree of completeness, it will best serve to give an idea of the essential anatomical characters of the group.

Medullosa anglica is derived from the Lower Coal-measures of Lancashire, at the same horizon to which most of our British Coal-plants, with structure preserved, belong. The original specimens were found in nodules from the coal-seam at the Hough Hill Colliery, Stalybridge, at dates ranging from 1892 to 1898, by the late Mr. G. Wild and Mr. Lomax.¹ It is a curious fact that these specimens were the first stems of a *Medullosa* to be recognised in this country, though the petioles of plants belonging to this genus had long been familiar among the common objects of the calcareous nodules. Specimens have since been found in other localities, and it is interesting that at Shore, Littleborough, they occur in

¹ For a fuller description, see my paper, "Structure and Affinities of Fossil Plants from the Palaeozoic Rocks: iii. *Medullosa anglica*, a New Representative of the Cycadofilices," *Phil. Trans.* vol. 191, B, 1899.

the roof-nodules, which often show a distinct Flora from that of the nodules in the seam below.¹

The stems are of rather large size, having a mean diameter of 7 or 8 cm., in the specimens at present known. This dimension includes the leaf-bases, which were adherent to the stem for a long distance before becoming free ; in fact, practically the whole external surface was formed by these leaf-bases, which were spirally arranged,

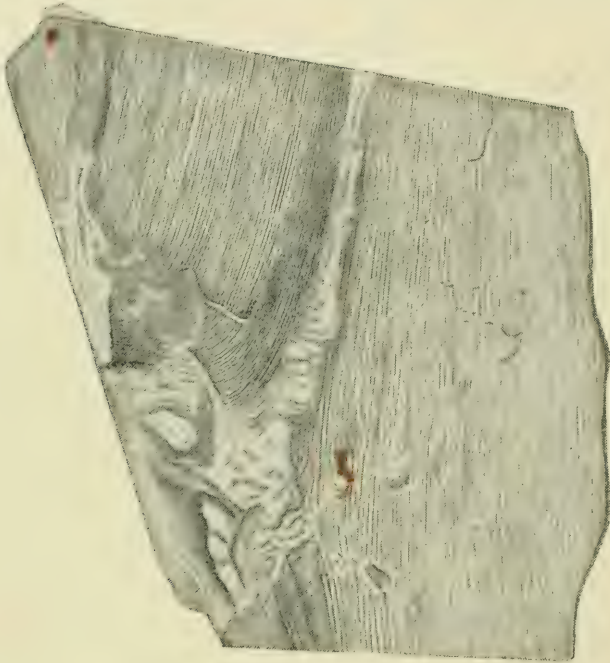


FIG. 70.—*Medullosa anglica*. External view of stem, showing two large leaf-bases, with a furrow between them. The surface is ribbed, owing to the presence of hypodermal strands of sclerenchyma. $\frac{2}{3}$ nat. size. S. Coll. (G. T. G.)

the phyllotaxis, where it could be determined, having followed the $\frac{2}{3}$ arrangement. Fig. 70 will give an idea of the external appearance of the fossil stem ; the surface of the large adherent leaf-bases is marked by a longitudinal striation, due to the hypodermal ribs of sclerenchyma, which stand out prominently in the fossil,

¹ Dr. Arber described in 1903 a specimen in the Binney Collection at Cambridge. This must have been discovered many years before the type-specimens, but had apparently lain unnoticed. See Arber, "On the Roots of *Medullosa anglica*," *Ann. of Bot.* vol. xvii. 1903.

though during life they must have been nearly or quite concealed from view by overlying tissue. The transverse section, represented somewhat diagrammatically in Fig. 71, shows the chief points in the organisation of the stem. This section was cut near the bottom of a piece of stem about a foot long. At this level, three large leaf-bases are shown; that marked *c* in the figure is the nearest to its separation from the stem, and actually became free an inch or two higher up. The next leaf

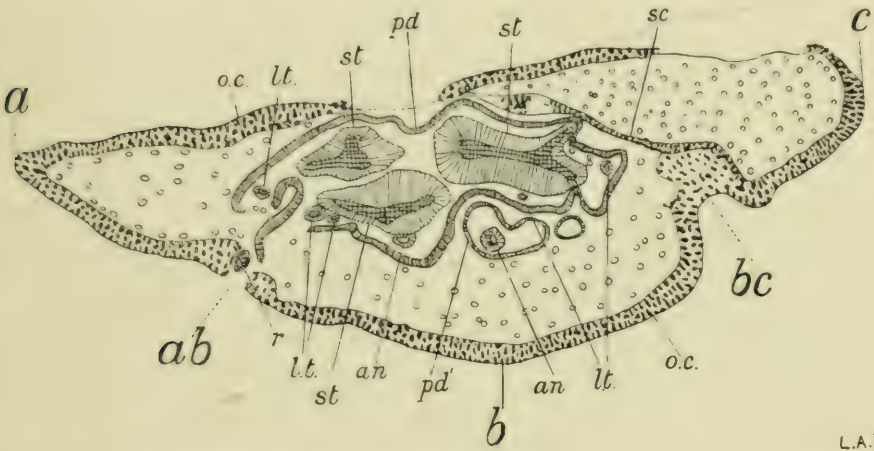


FIG. 71.—*Medullosa anglica*. Transverse section of stem, showing three large leaf-bases, *a*, *b*, and *c*. *ab*, *bc*, position of next leaf-bases above. *st*, the three steles; *lt.*, leaf-traces; *an*, accessory rings of wood and bast; *pd*, periderm, forming a ring round the group of steles, and also enclosing one of the accessory strands; *r*, adventitious root; *o.c.*, hypoderma; *sc*, sclerenchymatous band between leaf-base and stem. Slightly reduced. *Phil. Trans.*, S. S. Coll. 737.

to become free is that marked *b*, while *a* remains in connection with the stem for a vertical distance of 5 or 6 inches. At higher levels, two new leaf-bases make their appearance, the first (*bc*) between *b* and *c*, and the next (*ab*) between *a* and *b*. Thus the order of insertion of the leaves from below upwards was *c*, *b*, *a*, *bc*, *ab*, an arrangement which implies a $\frac{2}{5}$ phyllotaxis. The habit of the stem, clothed with its large adherent leaf-stalks, may well have resembled that of some of the Tree-ferns.

Coming now to the internal structure of the stem, we find that its organisation resembles that of the majority

of the Ferns, in being of the so-called *polystelic* type.¹ The number of the steles in *M. anglica* is normally three (see Fig. 71, *st*) ; each has a somewhat elongated and irregular transverse section ; traced longitudinally, they divide and again fuse with one another at long intervals. The structure of the individual stele is almost identical with that of the single vascular cylinder of a *Heterangium*. The central part of each stele is completely occupied by the primary wood, consisting of groups of tracheides intermixed with conjunctive parenchyma. The primary tracheides are for the most part pitted, just as in *Heterangium* ; the spiral tracheides of the protoxylem, accompanied by a few scalariform or reticulated elements, occur in several groups near the outer margin of the primary wood (see Fig. 72, which includes parts of two steles).

Each stele is surrounded separately by its own zone of secondary wood and bast (Figs. 71 and 72, *x*², *ph*), so that we have in this family a combination of polystelic structure with normal secondary growth of the individual stele. This is the great anatomical character of the genus *Medullosa*, with its immediate allies, and separates them at once from all plants now living, though, as we have seen, there is one other fossil family (that of the *Cladoxyleae*) which shares the peculiarity (see p. 156). It will be noticed that in *M. anglica*, as in certain *Cladoxyleae*, the development of secondary wood is commonly greatest on the side towards the centre of the stem.

The secondary wood has the same structure as in *Heterangium* or *Lyginopteris* (see Fig. 72). The tracheides, which are in radial series, accompanied by muriform medullary rays, are, as a rule, pitted on their radial walls only. The pits are multiseriate and bordered,

¹ I have adhered to the now familiar terms "polystely" and "polystelic," but they are used in a purely descriptive sense, without any implication that each of the several steles is to be regarded as homologous with the single stele of a typical monostelic stem.

just as in the genera last mentioned. Only slight remnants of the cambium are preserved, but sufficient to show that it was in the normal position, forming wood internally and phloem externally, with reference to each stele. The phloem itself is fairly preserved in places (Fig. 72, *ph*), and consisted of strands of long

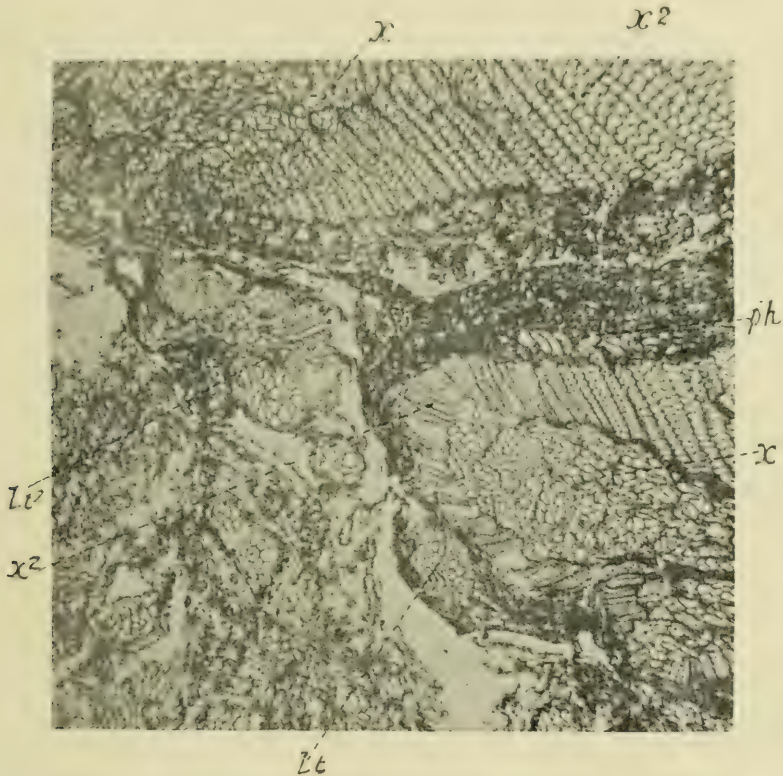


FIG. 72.—*Medullosa anglica*. Part of transverse section, showing portions of two steles, and leaf-traces going off from them. *x*, primary wood of steles; *x*², secondary wood; *ph*, phloem; *Lt.*, leaf-trace, just detached from its stele; *Lt*²., large leaf-trace, beginning to divide. Other smaller bundles are shown. $\times 10$. *Phil. Trans.*, S. From a photograph. S. Coll. 579.

tapering elements, clearly the sieve-tubes, forming a network, the meshes of which were occupied by the rather wide phloem-rays. In the Binney specimen, described by Dr. Arber, the sieve-tubes are perfectly preserved, and have conspicuous sieve-plates on their lateral walls, just as in *Heterangium tiliacoides*.¹ There

¹ Arber, *loc. cit.* Plate xx. Fig. 4.

appears to have been a pericycle around each stele, but its structure is ill-preserved.

So far, the general organisation of *Medullosa anglica* may be roughly described as that of a polystelic *Heterangium*. In the points which remain to be described, the *Heterangium* type is departed from more widely; the differences are partly correlated with the polystely, and partly depend on the greater size and complexity of the plant as a whole.

The leaf-trace bundles were given off, for obvious reasons, only from the free, peripheral side of the steles. Where a leaf-trace first becomes free from the stele, it is a large bundle, to all appearance truly concentric in structure (see Fig. 72, *l.t.*). It consists of a central mass of primary wood, with one or more protoxylem-groups near its external margin. This is surrounded by a zone of secondary wood and phloem. The primary wood of the leaf-trace is continuous with the outer part of that of the stele from which it springs. As the leaf-trace passes upwards and outwards through the cortex it loses its secondary tissues, and divides up repeatedly (Fig. 72, *l.t.*²) to form a number of smaller bundles, each of which eventually assumes a collateral structure. These ultimate leaf-trace bundles have their protoxylem directed outwards, adjoining the phloem (see Fig. 73, in which two exceptionally well-preserved collateral bundles are shown); their xylem usually consists of spiral and finely scalariform elements only, the pitted tracheides, which are abundant in the undivided leaf-traces, disappearing as the ramification of the bundle goes on.

The cortical tissues of the stem require no detailed description; they consist of short-celled parenchyma, traversed by numerous secretory canals, much resembling the gum-canals of recent Cycads.

A zone of internal periderm was formed around the central part of the stem, enclosing the group of steles,

and separating them from the outer cortex and leaf-bases (Fig. 71, *pd*). The periderm was morphologically comparable to cork; it is extremely well preserved, and was evidently formed wholly or chiefly on the external side of the phellogen. How far the tissue was actually suberised is doubtful; the good preservation of parts lying outside the periderm suggests that true cork had not yet been formed.

In one specimen, apparently forming part of an old

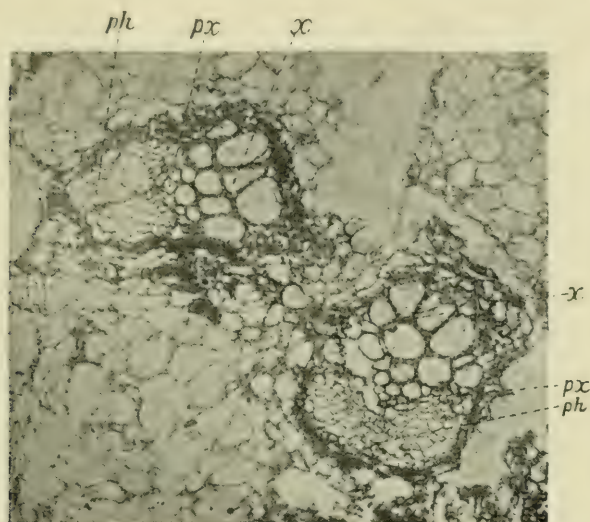


FIG. 73.—*Medullosa anglica*. Two leaf-trace bundles from the outer cortex of the stem, in transverse section, showing collateral exarch structure. *px*, protoxylem; *x*, centripetal xylem; *ph*, phloem. $\times 35$. *Phil. Trans.*, S. From a photograph. S. Coll. 579.

stem, the whole of the outer cortex, together with the leaf-bases, had been exfoliated, leaving the periderm exposed. It may be doubted, however, whether this exfoliation was a normal process.

A point of some anatomical interest is the occasional presence, in the cortex, of accessory vascular strands, of concentric structure, and probably of wholly secondary origin (Fig. 71, *an*). These formations recall the similar cortical bundles occurring in the genus *Cycas* and some other members of the Cycadaceae at the present day.

The petioles of *Medullosa anglica* were of large size,

having a diameter of 4 cm. or more, at the point where they became free from the stem. Each leaf-stalk received a large number of vascular bundles, as many as seventy or eighty in all, derived from the repeated ramification of several of the principal leaf-traces. The supply of bundles did not all enter the leaf-base from the stem at the same level; they passed in successively, in groups corresponding to the various principal leaf-traces from which they were derived. Thus their number, in the leaf-base, increased from below upwards. At a certain height, however, the leaf-base was marked off from the interior of the stem by a band of internal sclerenchyma, and above this level no more bundles were received (see Fig. 71, *c*). The petiole, where it first detaches itself from the stem, has the following structure (Fig. 74, *A*): On the extreme outside we may find a layer or two of palisade-like tissue (rarely preserved), which probably served for assimilation. Within this is the broad hypodermal zone (*hy*), consisting of numerous vertical strands of fibres, interspersed with parenchyma, and accompanied by secretory canals of the usual Cycadean type.

The whole interior of the leaf-stalk is occupied by a short-celled ground-tissue, containing secretory canals (*mc*), and traversed by the numerous vascular bundles (*v.b.*), ranged more or less regularly in concentric circles. The general structure was, in fact, much like that of the petiole of a recent Cycad. The individual bundles likewise resemble those of the recent family, differing only in the fact that their xylem was entirely centripetal, while in a modern Cycad a small amount of centrifugal wood is also present. This difference, however, does not seem to have been an absolutely constant one, for in some of the Medulloseae the foliar bundles are described as having precisely the Cycadean structure.

Petioles of the kind described have long been known under the generic name of *Myeloxylon*; the particular

form belonging to our *Medullosa* resembles that named by M. Renault *Myeloxylon Landriotii*, distinguished chiefly by the multiseriate arrangement and elliptical transverse section of the fibrous hypodermal strands.

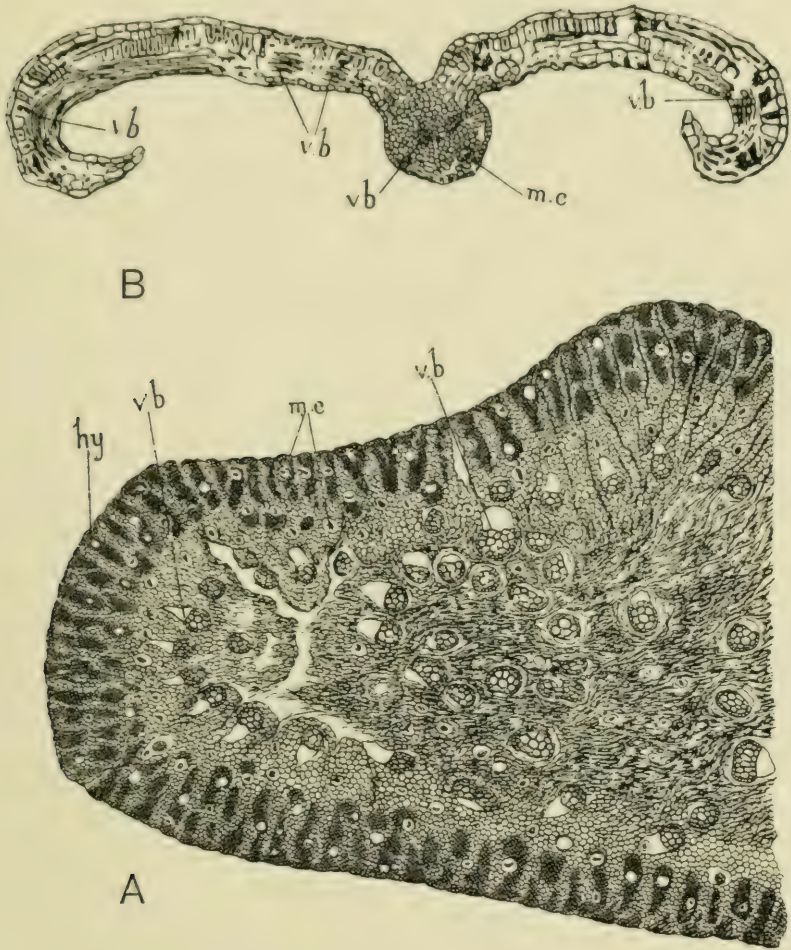


FIG. 74.—*Medullosa anglica*. A. Transverse section of petiole, showing the numerous vascular bundles, *v.b.*; *m.c.*, mucilage-canals; *hy*, hypodermis, with sclerenchymatous ribs. The whole has the structure of "*Myeloxylon Landriotii*." \times about 8. S. Coll. 686. (G. T. G.) B. Vertical section of leaflet. *v.b.*, vascular bundles of mid-rib, and lamina; *m.c.*, mucilage-canal. Palisade-tissue shown towards upper surface. \times 28. *Phil. Trans.*, S. S. Coll. 691.

The same petiolar structure, however, was no doubt common to certain other species of *Medullosa*. The fact that the fossils named *Myeloxylon* are nothing but the petioles of *Medullosa* had previously been proved, by

Weber and others, for one of the Continental species.¹ In the case of *M. anglica* the conclusion is perfectly obvious, for the leaf-bases, still attached to the stem, show in all respects the typical *Myeloxylon* structure. The genus *Myeloxylon* is therefore one of those which can now be dispensed with, or at most be retained, as a matter of convenience, for those petioles which have not yet been referred to their particular species of *Medullosa*.

The petioles of *Medullosa anglica* were of great length, and branched repeatedly, the successive branches diminishing in size, and undergoing some simplification in structure. The whole evidently constituted the rachis of a highly compound, probably bi- or tripinnate leaf. The final ramifications, which are no more than a millimetre in diameter, contain only a very few vascular bundles, but these still retain the same collateral, exarch structure as those of the main petiole. Gum-canals occur throughout the rachis; the hypodermal structure becomes simplified in the finer branches, consisting of an almost continuous zone of peripheral sclerenchyma.

Associated with the branched rachis, leaflets of characteristic structure are found. As shown by transverse sections, these leaflets are constantly revolute at their margins (see Fig. 74, B); the parenchyma towards the upper surface is of palisade-like structure, while the lower portion of the mesophyll is more lacunar. The lateral bundles, which traverse the lamina in an oblique direction, are accompanied by fibrous elements. The midrib is very prominent on the lower surface, and shows the same structure as a small branch of the rachis. From constant association and agreement in structural details, there is no doubt that these pinnules formed part of the *Medullosa* leaves. This conclusion is of

¹ See Weber and Sterzel, *Beiträge z. Kenntnis der Medulloseae*, Chemnitz, 1896. The original discovery was made by Weber about the year 1880.

great interest, because the pinnules in question agree closely with certain leaflets described by M. Renault in 1883, which, as shown by their external characters, belonged to an *Alethopteris*.¹ The rachis and petiole of M. Renault's *Alethopteris* showed the anatomical structure of "*Myeloxylon Landriotii*." Thus the French author's observations, taken in conjunction with Weber's discovery that "*Myeloxylon Landriotii*" was the leaf-stalk of a *Medullosa*, proved that the well-known *Alethopteris* fronds were borne as foliage on certain of the *Medullosa* stems.

From the organisation of the petioles and leaves in *Medullosa anglica*, there can be little doubt that the English species also bore foliage of the *Alethopteris* type, an example of which is illustrated in Fig. 69 from *A. lonchitica*, very probably the actual species concerned.

The roots of *M. anglica* have frequently been found in connection with the stem, on which they were borne in vertical series, between the leaf-bases. They have a normal triarch structure, and, with increasing age, formed a large amount of secondary wood and bast, interrupted opposite the protoxylem-angles by large medullary rays, just as in recent roots with secondary growth. The detailed structure of the xylem agrees with that of the corresponding tissue in the stem. Dr. Arber found that the phloem much resembled that in the stem of *Heterangium tiliacoides*. The groups of sieve-tubes are accompanied by phloem-parenchyma, and separated by dilated parenchymatous rays. The sieve-tubes show the lateral sieve-plates particularly well; ² this appears to be the only case in which this structure has been recognised in the root of a fossil plant. A very characteristic feature of these roots, with the exception of the youngest specimens, is the presence of a wide zone of large-celled periderm, forming the external

¹ Renault, *Cours de botanique fossile*, vol. iii. p. 159, Plate xxvii.

² Arber, *loc. cit.* Plate xx. Fig. 5.

covering of the organ. Developmental stages have been observed, proving that the periderm was an internal one in origin, arising by division of the pericyclic cells, and thus causing the exfoliation of the whole cortex. A small amount of phelloderm was formed on the inner side of the cork-cambium.¹ In all respects the roots of *Medullosa anglica* agree with those of recent Gymnosperms.

The larger roots reached a diameter of about half an inch. They branched pretty freely, giving off rootlets of various orders. The xylem of the rootlet was always inserted on an angle of the primary wood of the main root, in the way normal for these organs.

If we now sum up our knowledge of the vegetative organs of *Medullosa anglica* we find that it had a polystelic stem, each of the steles, usually three in number, resembling, as regards both the primary and secondary tissues, the single central cylinder of a *Heterangium*.

Externally, the stem was clothed by the bases of the large, spirally disposed leaves, which were repeatedly compound, and no doubt presented the external characters of an *Alethopteris*, with which they agree in anatomical structure.

Each leaf received from the stem a large number of vascular bundles, derived from the repeated subdivision of a number of the principal leaf-traces springing from the steles. The principal leaf-traces were concentric in structure, and surrounded by secondary wood and bast, but, as the bundle underwent subdivision, its branches gradually lost their secondary tissues, and, at the same time, assumed a collateral, exarch structure. The petiole and rachis had in all respects the structure of "*Myeloxylon Landriotii*." The stem bore triarch, adventitious roots, forming secondary wood and bast, and coated by a periderm of pericyclic origin.

The form of *Medullosa* just described, which happens

¹ Arber, *loc. cit.* p. 428, Plate xx. Fig. 2.

to be the one most completely known up to the present time, represents the genus, as it were, in its simplest expression.

Some other species or provisional species of a similar type have been recorded. One of these, *Medullosa pusilla*,¹ from the Soap-stone of the Lower Coal-measures, was found by Mr. P. Whalley at Colne, Lancashire. It is probably the smallest *Medullosa* on record, the stem, with the leaf-bases, having been only 2 cm. in diameter. The structure is in most respects the same as in *M. anglica*; the hypoderma of the leaf-base, however, has a simpler construction, and it is doubtful whether the leaf-trace, on leaving the stele, had any secondary tissues of its own. It is probable, though by no means certain, that the species may be distinct.

Another form, described by Dr. Ethel de Fraine, under the name *M. centrofilis*,² is of greater interest. The specimen came from the Lower Coal-measures of Shore, Littleborough. In dimensions it is intermediate between *M. anglica* and *M. pusilla*, measuring in its flattened condition 5×1.5 cm. The general structure here also is much like that of *M. anglica*; there are three or locally four main steles, but in the middle there is a small cylindrical stele, comparable to one of the "star-rings" characteristic of the complex Permian species, to be described immediately. The central stele was not observed to undergo any fusion with its neighbours, or other change in the length of stem available for investigation. Its presence indicates a somewhat higher differentiation than has otherwise been observed among the Lower Coal-measure forms. In *M. centrofilis* the undivided leaf-traces are without secondary tissues, as appears to have been the case in *M. pusilla* also. The

¹ D. H. Scott, "On *Medullosa pusilla*," *Proc. Royal Soc. B*, vol. 87, 1914, p. 221.

² E. de Fraine, "On *Medullosa centrofilis*, a new species of *Medullosa*, from the Lower Coal-measures," *Ann. of Bot.* vol. xxviii. 1914, p. 251.

primary xylem was probably exarch, not mesarch, a point which could not be determined for certain in *M. pusilla*.

In the Renault collection at Paris there are sections, under the name *Heterangium geriense*, of the stem of a *Medullosa*, apparently of the same type as *M. anglica*, from the Upper Coal-measures of the Ride de Gier, near St. Etienne. This species may bear the name *Medullosa geriensis*.

All these forms, *M. pusilla*, *M. centrofilis*, and *M. geriensis*, belong to the group or "form-cycle" of which *M. anglica* is the type.¹

Several Continental species had previously been investigated, all of which are of later geological age than *M. anglica*, belonging chiefly to the Permian beds (see the diagrams in Fig. 75). They all have a more complex vascular system than the English species; the steles are usually more numerous, and in all cases show a differentiation among themselves. The larger steles are associated to form a single or double peripheral ring, while others, of much smaller size, are grouped in the central region of the stem. In most of the specimens, as, for example, in those of the form-cycle known as *Medullosa stellata* (Fig. 75, D, F, and G), the peripheral steles are few in number, or even reduced to one, and much elongated in the tangential direction, so as to form an almost continuous ring, with few, if any, interruptions. In some cases the peripheral ring appears to have been completely unbroken, forming a single solenostele, such as we find in various recent Ferns and Fern-allies, as, for example, in *Loxsonia*, *Dicksonia*, and *Marsilia*. In all cases, however, so far as satisfactory investigations have been made, the structure of the individual stele is essentially like that in *Medullosa anglica*. The interior (the so-called "partial pith") is occupied by primary wood, often associated with a rather large amount of parenchyma,

¹ Cf. E. de Fraine, *l.c.* 1914, p. 262.

and this is surrounded on all sides by secondary wood and phloem. It is a curious feature, however, that most of the primary tracheides commonly run in a tangential direction instead of vertically.¹ The small central steles usually have an approximately circular transverse section; they anastomose both among themselves and with the peripheral steles, which they resemble in structure. We see, then, that in all these forms of *Medullosa* the structure of the stem was polystelic, as in the simpler species, *M. anglica*, with which we started. The differentiation of the steles into a central and peripheral system marks, however, a distinct advance on the part of the later representatives of the genus. The outer, more or less continuous, stelar zone allowed of indefinite growth in thickness, on its free external side. It is the rule, in the older stems of the type of *Medullosa stellata*, to find that the great bulk of secondary wood and bast was developed on the outer side of the peripheral steles; on the inner side of the same zone, and around the small central steles, the growth was of necessity limited by want of space. Consequently, an old stem of *Medullosa stellata* may assume a very different appearance, as seen in transverse section, from that typical of the genus, the external wood and bast predominating so largely over all the other tissues that the original polystelic organisation sinks, as it were, into the background.

In some exceptional instances additional complications made their appearance. This was the case, for example, in a huge specimen of *Medullosa stellata* (var. *gigantea*), the largest as yet discovered, the stem of which, though decorticated, was over a foot and a half thick. The central ground-tissue, 5 or 6 inches in diameter, was traversed by forty-three central steles, some of which were an inch in diameter. The peripheral zone

¹ See Rudolph, "Zur Kenntnis des Baues der Medullosen," *Beihefte z. Bot. Centralblatt*, Bd. xxxix. Abt. ii. 1922.

of steles was enormously thickened on its outer surface, but, in addition to this, there were three concentric extra-fascicular layers of normally orientated wood and bast which had been formed successively around the whole of the polystelic vascular system. Thus, in such specimens, the anomaly characteristic of the recent Cycadean genera, *Cycas*, *Macrozamia*, and *Encephalartos*, coexisted with the polystelic structure of a *Medullosa*.¹

It is evident that some of the Permian Medulloseae reached the dimensions of fair-sized trees ; others appear to have had long and comparatively slender stems ; it has been conjectured that some of the latter may have been climbers, like the lianes of tropical forests, but for this supposition there is no real evidence. The resemblance of the anatomical structure of the Medulloseae to that of the stems of certain climbing Sapindaceae, pointed out in 1881 by Göppert and Stenzel,² is more apparent than real. Some of the Sapindaceous lianes have a number of vascular cylinders in the mature stem, but this is merely an anomaly of secondary growth, depending on the peculiar distribution of the cambium ;³ the whole structure is no doubt an adaptation to a climbing habit. In *Medullosa* the primary organisation was evidently polystelic (dialystelic), as in most recent Ferns, and there is no reason to assume that it had any relation to scandent growth.

It may be pointed out here that the polystely of *Medullosa* differs from that of the typical polystelic or dictyostelic Ferns in having, so far as appears, no relation to the presence of " leaf-gaps." In the species at present investigated the leaf-traces of *Medullosa* are given off from the outer faces of the steles, and leave no gaps ; the breaking up of the original stele depended on some

¹ See Weber and Sterzel, *l.c.*

² " Die Medulloseae, eine neue Gruppe der fossilen Cycadeen," *Palaeontographica*, 1881.

³ Cf. De Bary, *Comparative Anatomy of Phanerogams and Ferns*, English edition, 1884, p. 581.

other cause. Further investigation is necessary to show whether this distinction is absolute.

In one or two of the Continental *Medulloseae* something has been ascertained as to the course of the leaf-traces; thus, in *M. stellata*, the leaf-traces are given off from the peripheral steles, and each is at first surrounded by its own zone of secondary wood (Fig. 75, G). They then divide up, lose their secondary tissues, and become collateral, just as in *M. anglica*. They have not, however, been traced into the petioles, which are as yet unknown in *M. stellata*.

In another Continental species, *M. Leuckarti*¹ (Fig. 75, H), the leaf-traces behave in the same way, though their connection with the steles appears not to have been seen at present. In *M. Leuckarti* the structure of the leaf-bases is known, and, as in the English species, is of the type of "*Myeloxylon Landriotii*."

In both the species of *Medullosa* just mentioned the leaf-traces are given off from the outermost steles. In *M. Solmsii* (Fig. 75, E, L), however, where there is a double zone of peripheral steles, the bundles arise from the inner ring. In no case were the more central cylindrical steles directly connected with the leaf-traces, though there was indirect communication, by means of fusions with the peripheral system.

Our knowledge of the foliage of the Continental *Medullosae* is a matter of inference. *M. Leuckarti*, as already mentioned, bore leaf-stalks with the structure of "*Myeloxylon Landriotii*," and we know, from M. Renault's researches, that petioles with that structure belonged to *Alethopteris*. There is therefore a strong presumption that the foliage of *Medullosa Leuckarti*, like that of *M. anglica*, was of the *Alethopteris* type. *M. Leuckarti* seems to have had a short stem, and may have been of almost herbaceous habit. From the structure of the leaf-traces in *M. stellata*, which includes the

¹ Solms-Laubach, "Über *Medullosa Leuckarti*," *Bot. Zeitung*, 1897.

largest specimens of the genus, there is little doubt that its petioles were also of the "*Myeloxylon*" kind, but we have no more direct evidence as to the nature of the leaf.

"*Myeloxylon*" petioles, of the type named by M. Renault *M. radiatum*, characterised by the radially elongated hypodermal bands of sclerenchyma, were shown by him to belong to the genus *Neuropteris*. There is therefore strong evidence that the latter genus, as well as *Alethopteris*, consisted, wholly or in part, of the foliage of species of *Medullosa*. Fern-like leaves of certain other genera, such as *Odontopteris*, *Callipteris*, and *Taeniopteris*, have been found in association with stems of the same type.

It will be useful, at this point, to state briefly the distinctive characters of the chief Continental species or "form-cycles," as they were called by Sterzel and Weber, of *Medullosa*. The genus was founded by Cotta,¹ in 1832, on specimens from the Permian of Saxony; he distinguished three species, *M. elegans*, *M. porosa*, and *M. stellata*. Only the two latter, however, are really stems, the *Medullosa elegans* of Cotta has turned out to be a petiole (*Myeloxylon*, Brongniart) belonging to the same genus. At present we may consider four species of the Continental type as well established, while a fifth (*M. gigas*) is more doubtful.

In *M. stellata*, Cotta (Fig. 75, D, F, C), the outer stele or steles form a more or less continuous peripheral ring; in the older stems the centrifugal, external zone of secondary tissue is considerably more developed than the inner centripetal portion. The central cylindrical steles or "star-rings" are fairly uniform in structure and evenly thickened all round; they vary much in number, from forty-three in the large trunk already mentioned, down to a single one in the form described

¹ C. B. Cotta, *Die Dendrolithen in Beziehung auf ihren inneren Bau*, Dresden und Leipzig, 1832.

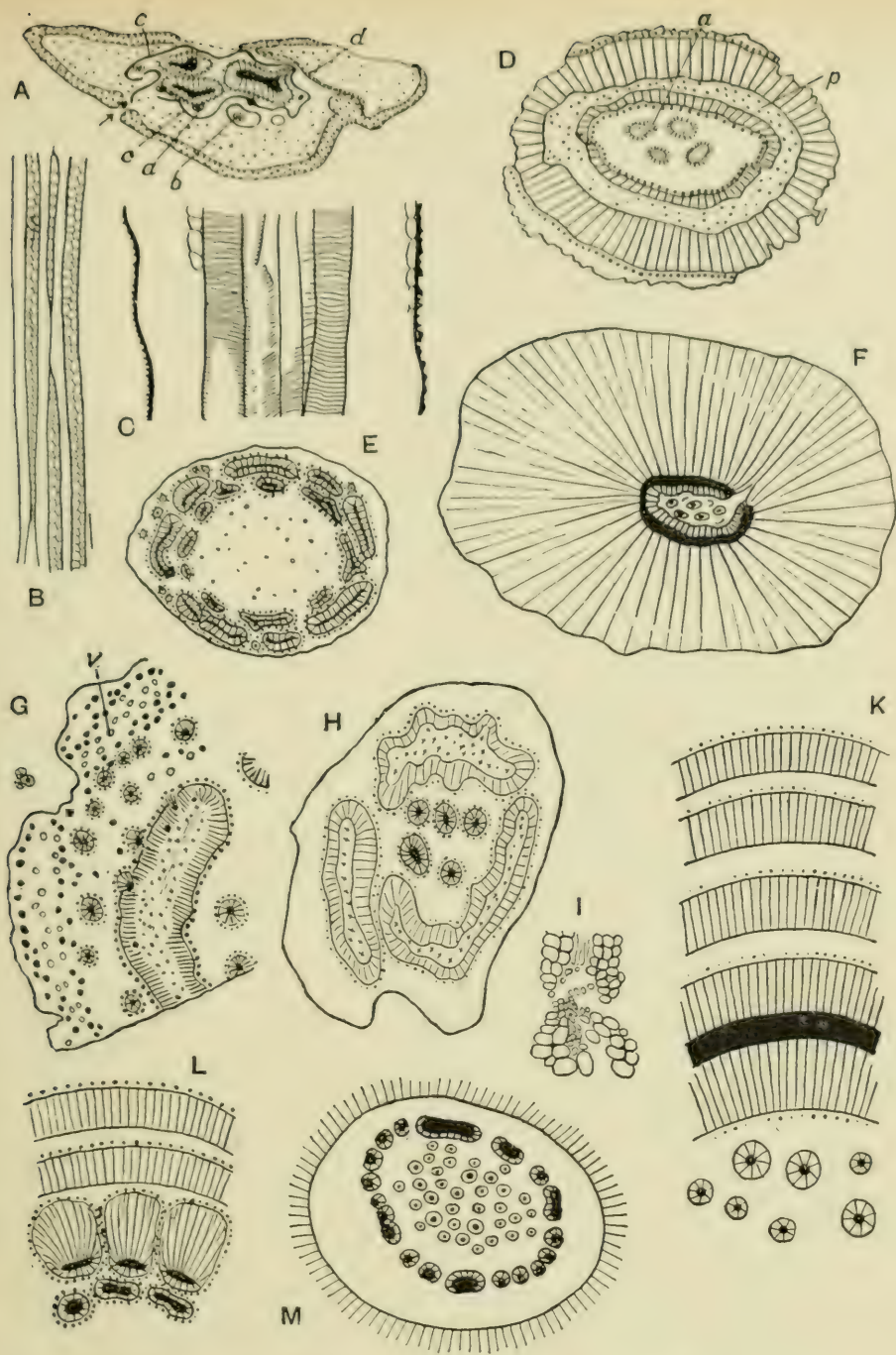


FIG. 75.—*Medullosa*, stems. Reproduced from Seward's *Fossil Plants* (Cambridge Univ. Press) by permission. A-C. *M. anglica*. A. Transverse. *a*, *b*, accessory strands; *c*, periderm; *d*, sclerenchyma (see Fig. 71). B. Part of secondary wood in tangential section. C. Primary xylem. D. *M. stellata*, transverse; *a*, star-rings; *p*, "partial pith" of solenostele (after Weber and Sterzel). E. *M. Solmsii*, transverse (after Weber and Sterzel). F. *M. stellata*, with enormously thick outer wood of peripheral stele (Brit. Museum Coll., No. 13767). G. *M. stellata*, var. *corticata*, showing some steles and cortex. *v*, leaf-trace bundles (after Weber and Sterzel). H. *I. M. Leuckarti*. H, transverse, showing central and peripheral steles. I. transverse from interior of a stele, showing primary wood below and secondary above (after Weber and Sterzel and Solms-Laubach). K. *M. stellata*, var. *gigantea*, transverse; star-rings below; *a*, part of peripheral stele; *b-b*, successive layers of extra-fascicular wood (adapted from Weber and Sterzel). L. *M. Solmsii*, var. *lignosa*, transverse, showing part of the double zone of steles, and of two extra-fascicular layers. M. *M. porosa*, transverse, showing the two kinds of central steles and the inner edge of the peripheral stele. (L, M, after Weber and Sterzel.) All from Seward. Block lent by the Cambridge University Press.

by Sterzel and Weber as *M. stellata*, var. *lignosa*. In the latter case we have the same condition as in the British species, *M. centrofilis*, so different in other respects.

In the largest stems, as already mentioned, the normal secondary thickening of the steles may be supplemented by the appearance of successive extra-fascicular zones of wood and bast (Fig. 75, K).

The *Medullosa gigas* of Renault (*Palaeoxylon*, Brongniart), from the Permian of Autun in France, is founded on fragments of large trunks, in which little but the secondary wood is preserved. There is scarcely any trace of the internal centripetal layer of wood, which should be present if the structure were on Medullosean lines, but in some specimens circular or elliptical strands have been recognised in the pith recalling the "star-rings" of other species. The stem, if correctly referred to *Medullosa*, appears to be the largest known in the genus.¹

Medullosa porosa, Cotta, is a species closely allied to *M. stellata*, with which it agrees in the structure of the peripheral stelar zone. The difference lies in the internal steles or "star-rings"; they are numerous and differentiated into two distinct zones (Fig. 75, M). The more central "star-rings" are small and regular like those of *M. stellata*; the outer ring, however, consists of larger steles, often fused together, with the remarkable peculiarity that their secondary thickening is chiefly or even wholly limited to the *inner* side. It will be remembered that the same feature was met with in the steles of the British Lower Coal-measures species. Anastomosis takes place, not only among the "star-rings" of the outer zone, but also between the latter and the steles of the central group.

Medullosa Solmsii, Schenk, is a very different species from those just described. The peripheral steles or

¹ Renault, "Bassin houillier et permien d'Autun et d'Épinac," *Flore fossile*, ii, p. 297, Pl. lxxi. 1893-1896.

"plate-rings" are numerous and distinct, and are ranged in two concentric circles, those of the outer circle being the larger (Fig. 75, E). In the central pith of the stem there are many minute cylindrical steles or "star-rings" of the usual structure; these, however, are unimportant compared with the main peripheral system. The primary wood of the various steles seems to have been little developed, and the secondary wood is of denser structure than in other species. As already mentioned, it is from the inner of the two peripheral circles of steles that the leaf-traces are given off; they pass outwards through the gaps between the steles of the outer zone (Fig. 75, E).

In the older stems the wood of the outer steles becomes excessively thickened on the peripheral side, and, in addition, successive extra-fascicular secondary zones may be developed in the cortex (*M. Solmsii*, var. *lignosa*), just as in the largest form of *M. stellata* (Fig. 75, I).

The species *Medullosa Leuckarti*, Goepf. and Stenz., already described, is again very distinct. Here the peripheral vascular system of the stem consists of one or two zones of large steles, few in number; each stele, as seen in transverse section, has an irregular, sinuous form, which led the older writers to employ the expressive term "snake-rings" (Fig. 75, H). The steles have a wide "partial pith," consisting of the primary wood, intermingled with parenchyma; the secondary tissues do not attain any great thickness. A portion of the primary and secondary xylem of a stele is shown in Fig. 75, I.

In the middle of the stem there are several large "star-rings"; they appear to be budded off from the inner face of the peripheral steles. The leaf-trace strands and the *Myeloxylon* leaf-bases borne on the stem have been mentioned above.

Of all the continental species *M. Leuckarti* bears the nearest resemblance to the *M. anglica* type, with which

it agrees in many details ; it might well be described as an elaborated *M. anglica*, the species *M. centrofilis* forming a bridge between the two. The other Permian species give the impression of belonging to a distinct and more highly differentiated race within the genus *Medullosa*.

Colpoxylon.—A curious fossil stem, 15 cm. or more in diameter, from the Permian of Autun, in France, named by Brongniart *Colpoxylon aeduense*, and subsequently fully described and illustrated by Renault,¹ agrees in many respects with the simpler forms of *Medullosa*, but is peculiar in having, for a part of its length, a single vascular cylinder only (Fig. 76, 1). The stele has a very irregular outline, like the "snake-rings" of *M. Leuckarti*, and is surrounded by secondary wood and bast of the structure usual in Medulloseae. In the interior there are scattered groups of tracheides, for the most part running horizontally, and embedded in parenchymatous tissue.

Towards one end of the specimen the stele divides, first into two (Fig. 76, 2) and then into six or seven parts, so that the stem of *Colpoxylon* was monostelic in one part and polystelic in another. Internal "star-rings" are entirely absent. The leaf-trace bundles are preserved, and appear to agree essentially with those of *Medullosa* (cf. Figs. 72, 73). Their ultimate branches are collateral, and of the "*Myeloxylon*" type ; in some of them, centrifugal as well as centripetal wood has been found. The external surface of the stem bears a general resemblance to that of *Medullosa anglica* ; the leaves (except for their scars) are unknown. There can be no doubt that *Colpoxylon* belonged to the family Medulloseae ; possibly it may ultimately prove to have been simply an aberrant representative of the genus *Medullosa* itself. The local reduction of the vascular system of the stem to a single stele is the point of chief interest.

¹ *Flore fossile d'Autun et d'Épinac*, Part ii. p. 301, Pl. 66-68.

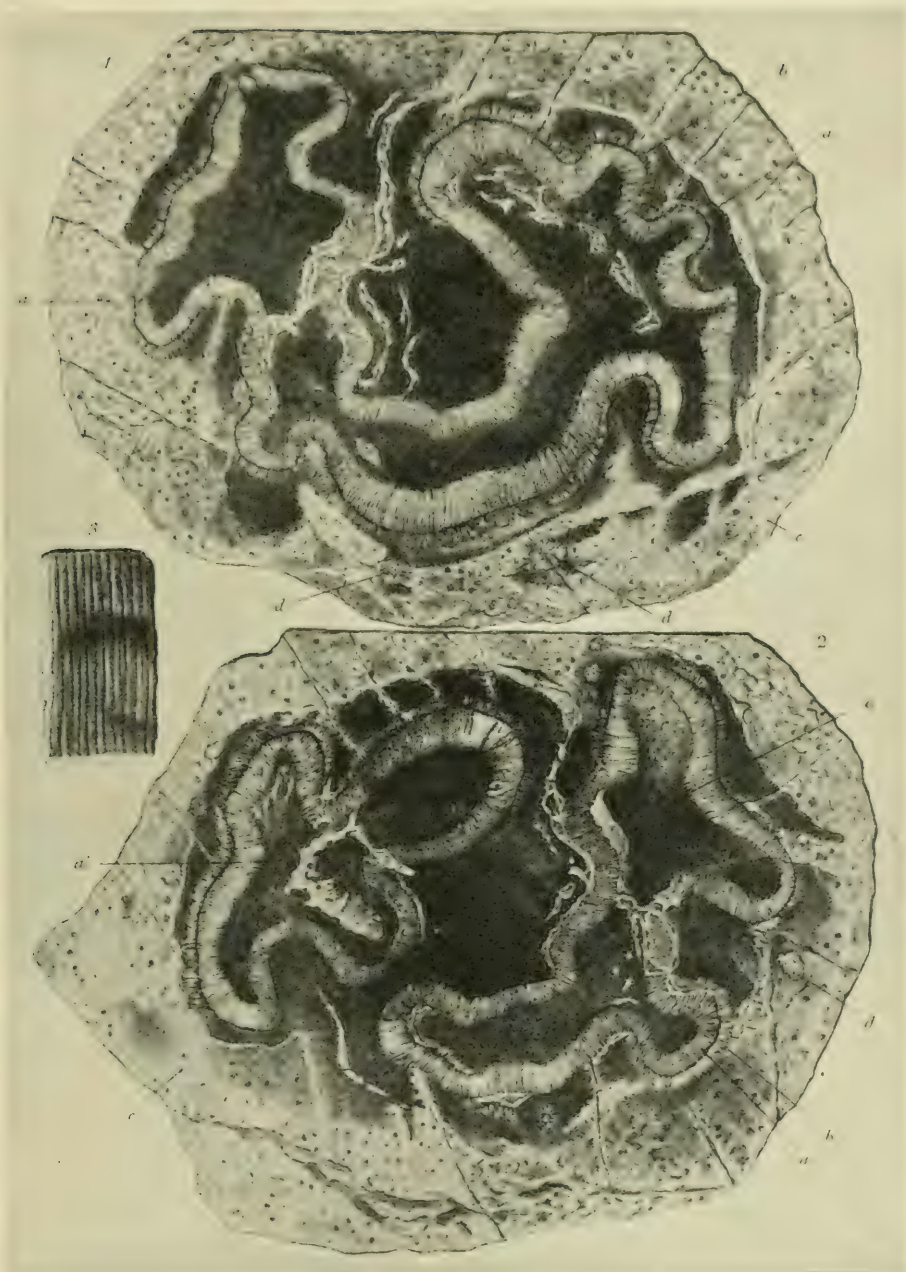


FIG. 76.—*Colpoxylon aeduense*. 1. Transverse of stem, showing the single, sinuous stele preparing to divide into two. *a*, *a'*, wood of stele; *b*, phloem, partially preserved; *c*, cortex, containing leaf-traces and sclerotic strands; *d*, stellate bundles, probably undivided leaf-traces. 2. The same, where the stele has divided into two. *a-d*, as in section 1. *e*, primary xylem-groups in "partial pith" of the steles. 3. Portion of external surface, about $\frac{1}{2}$ of natural size. From Renault.

There is some evidence that *Colpoxylon* was the stem of an *Alethopteris*,¹ though Renault thought that the gigantic simple leaves known as *Titanophyllum* might belong to it. Some original observations with new figures of *Colpoxylon* will be found in Prof. Seward's *Fossil Plants*, vol. iii. p. 142.

Sutcliffia.—Prof. Seward, in 1894, described, under the name of *Rachiopteris Williamsons*,² a petiole which bears a great general resemblance to "*Myeloxylon*," but differs from it (among other minor points) in the vascular bundles having concentric instead of collateral structure. Considering that in *Medullosa* the leaf-traces were, to all appearance, concentric on first leaving the steles, it was not surprising that in some forms they should have retained this structure after entering the petiole, and it thus appeared from the first highly probable that *Rachiopteris Williamsons* represented the leaf-stalk of some unknown member of the Medulloseae.

This conclusion has since been confirmed by the discovery of a new Medullosean stem (*Sutcliffia insignis*, Scott), first found by Mr. J. Lomax in material from Mr. Sutcliffe's colliery at Shore, Lancashire.³ *Sutcliffia insignis*, like Prof. Seward's fossil, is derived from the roof-nodules, where it is associated with Goniatile shells (see Fig. 77). A second specimen has since been described. The roof-nodule specimens no doubt represent the drifted fragments of a distinct flora, flourishing at some little distance from the coal-forming forests; to the latter the ordinary seam-nodules owed their origin.

The stem is a large one, measuring, in the type specimen, 12 × 6.5 cm. in diameter in its present somewhat

¹ Grand'Eury, " Sur les organes et le mode de végétation des Neuroptéridées et autres Ptéridospermes," *Comptes rendus*, t. cxlvi. p. 1243, 1908.

² *Annals of Botany*, vol. viii. 1894, p. 287.

³ Scott, " On *Sutcliffia insignis*, a New Type of Medulloseae from the Lower Coal-measures," *Trans. Linn. Soc. London*, 2nd ser. Bot. vol. vii. Part iv. 1906.



FIG. 77.—*Sulcitiflora insignis*. Transverse section of the stem and leaf-bases. At α , δ , and other places, meristemes are seen separating from the central stele. B , fused mass derived from two meristemes; B' , strand branching off from B ; ε , ε' , a strand previously detached; α' , two bundles derived from the meristeme α ; $v.b.$, two leaf-trace bundles fusing; $d.x.$, $d.x'$, double row of bundles probably marking the line along which a petiole will separate, higher up the stem. Very slightly enlarged. From a photograph by Mr. L. A. Boodle. Section lent by Prof. F. E. Weiss.

distorted condition. In a length of 9 inches, not more than one petiole leaves the stem, so the plant was presumably of a tall stature. The stem is clothed by large, spirally arranged leaf-bases, but detached petioles have been found greatly exceeding in size those borne by the stem, which must have been a comparatively small specimen—probably from a young plant. The second specimen, however, though older, is smaller.

The main feature of the anatomy, in which *Sutcliffia* differs from any Medullosean stem previously known, is the presence of a single central stele, of large size (measuring 4.7×1.8 cm. in the section figured, Fig. 77). There is no pith, and the wood has the same structure as in a stele of *Medullosa anglica*, except that in *Sutcliffia* the protoxylem-groups are peripheral, the xylem thus being exarch. A zone of phloem, in which strands of sieve-tubes can be recognised, surrounds the wood. In the stem first investigated (the only specimen then discovered) secondary growth was just beginning.

From the main stele, large, irregular strands, the meristeles or subsidiary steles, were detached at intervals, giving a remarkable and unique appearance to the transverse sections (see Fig. 77, *a*, *B*, and δ). The meristeles break up into smaller strands, but the main branches of adjacent meristeles often fuse with one another. Thus the large mass *B*, in Fig. 77, is the product of such a fusion, as shown by the comparison of serial sections. The strands derived from the further subdivision of the meristeles or their fused branches (Fig. 77, α' , β' , *B'*) ultimately constitute the numerous bundles of the leaf-trace (Fig. 77, *d.r.*, *v.b.*). The vascular strands in the leaf-bases and petioles always, however, retain a concentric structure, and their xylem contains parenchyma, so that they preserve a more stele-like character than the corresponding bundles in a *Medullosa*. The structure of the petiole agrees in all essentials, though not in every detail, with that of Seward's *Rachiopteris Williamsoni*,

which appears to be the petiole of another species of *Sutcliffia*, now called *S. Williamsoni*.

A second specimen of the stem, probably referable to the species *S. insignis*, was discovered in 1910 at Dearnley, in a mine adjacent to that from which the type-specimen was obtained. It was fully and admirably described by Dr. Ethel de Fraine in 1912.¹ This also was a roof-nodule fossil. It is a smaller stem than the type-specimen, measuring about 9.5×3.5 cm. in transverse dimensions as against 12×6.5 cm. in the type. It is true that the leaf-bases are lost in the Dearnley specimen, but the dimensions of the primary wood of the stele and meristeles are relatively small, and the specimen owes much of its present proportions to secondary growth. This is one of the great differences from the Shore stem; the latter was young, and secondary thickening had only just started; the Dearnley plant was almost in a senile condition, with an immense development of secondary wood, leading to the crushing and distortion of much of the primary xylem. The secondary zone reaches a thickness of 9 mm. in the stele, and is also predominant in the meristeles. In fact, one of the latter had thus grown to such abnormal dimensions that it might easily be taken for a second stele, if it were not that at a higher level it partly breaks up into leaf-traces.

Besides the great growth of the secondary tissues there are some other points in which the Dearnley specimen differs from the Shore plant. The most striking of these is the presence of a number of extra-fascicular vascular strands outside the normal system of stele and meristeles. These are arcs or concentric strands of secondary wood and bast, and appear to have no connection with the primary vascular system. The extra-fascicular formations always start from a cluster of

¹ E. de Fraine, "On the Structure and Affinities of *Sutcliffia*, in the light of a newly discovered specimen," *Ann. of Bot.* vol. xxvi. 1912.

isodiametric reticulate tracheides of large diameter. Such short tracheides, probably belonging to the pericycle, also occur elsewhere, in places where no secondary development had taken place.

The extra-fascicular strands of the Dearnley *Sutcliffia* fuse with one another to form a network. In structure they are practically identical with the accessory strands and arcs sometimes found in *Medullosa anglica*,¹ while they present a less close analogy with the external zones of thickening occurring in large stems of *Medullosa stellata* and *M. Solmsii*, and also have their parallel among recent Cycads.

Another feature of the Dearnley specimen is the presence of bands of periderm in the cortex. Dr. de Fraine was inclined to refer the absence of leaf-traces and outer cortex to this cause, the external tissues having been normally exfoliated, owing to cork-formation.

In the type-specimen, indications of cortical meristems, perhaps the precursors of periderm, have been noticed.

The peculiarities so far mentioned may all be explained by the more advanced age of Dr. de Fraine's specimen. One or two differences affecting the primary structure are also noted in her memoir. In the type-specimen fusions between distinct meristemes or their branches occur, as their course is followed in the upward direction. This was not observed in the second specimen, though the branches of the same meristeme may sometimes reunite; in one case a meristeme fused again with the main stele.

Dr. de Fraine also came to the conclusion that the meristemes were ultimately used up completely to form leaf-trace strands; in the type-specimen, where fusion took place, it seemed probable that a part of the meristeme persisted in the stem; these differences, if confirmed, might point to a specific distinction, though,

¹ See D. H. Scott, "On *Medullosa anglica*," *loc. cit.* p. 98.

on the other hand, there are so many details of structure common to both specimens as strongly to suggest specific identity.

Prof. Seward has judiciously solved the problem by distinguishing the two specimens as *forma a* and *forma β*.¹

Dr. de Fraine, while retaining the term "meristeles" for convenience, regarded these structures as essentially identical with the main leaf-traces of *Medullosa*. They are, however, so widely different in dimensions, form, and behaviour from ordinary leaf-traces, that they seem to demand a separate category, as subsidiary steles.

The vascular system of *Sutcliffia* has no parallel among any plants at present known, though a remote analogy may be traced with the anomalous structure of certain lianes belonging to the Sapindaceae. The genus is referred to the Medulloseae on account of the general organisation of the leaf-base and petiole, the numerous leaf-trace bundles, the tendency to dialystely shown in the formation of the subsidiary steles, and the histology of the vascular and cortical tissues.

The stem, however, has not deviated far from the monostelic condition, for the single central cylinder forms the dominant feature of the vascular system, while the meristeles serve to effect the transition to the leaf-traces. The plant is of considerable interest, as indicating the probable derivation of the Medullosean stem from a simple protostelic type, such as exists in *Heterangium* among the Lyginopterideae.

Further theoretical considerations will be postponed (p. 219).

FRUCTIFICATION OF MEDULLOSEAE.—There are at least two cases in which we have clear and direct proof that a member of the Medulloseae, or, as we should rather say, of the Neuropterideae, was a seed-bearing plant. In the same year in which the seed of *Lyginopteris* was

¹ *Fossil Plants*, vol. iii. p. 149, 1917.

first identified, Dr. Kidston was able to demonstrate the presence of seeds in a species of *Neuropteris*, one of the genera which Stur, twenty years before, had proposed to exclude from the Ferns.

In the well-known species *N. heterophylla*, the frond

of which is illustrated in Fig. 68 (p. 171), bodies considerably larger than a hazel-nut, and relatively longer, were discovered by Dr. Kidston, in nodules from the Middle Coal-measures of Dudley, attached to a rachis bearing the characteristic pinnules of *Neuropteris heterophylla*¹ (Fig. 78). He has since recorded other and more perfect specimens. They are casts, not petrifications, so no detailed study of structure has been possible, but the external characters leave no doubt that the organs in question are seeds. They are of the radially symmetrical type, and the



FIG. 78.—*Neuropteris heterophylla*. Seed, attached to a branch of the rachis bearing two characteristic pinnules. $\times 2$. After Kidston.

testa has a fibrous structure. Chiefly on account of the latter character Dr. Kidston refers the seeds to the genus *Rhabdocarpus* of Göppert and Berger.² The

¹ R. Kidston, "The Fructification of *Neuropteris heterophylla*," *Phil. Trans. Royal Soc. B*, vol. cxcvii. 1904.

² Brongniart, however, limited the genus *Rhabdocarpus* to seeds with bilateral symmetry (Platyspermeae of Oliver), see Fig. 92, p. 253.

seeds appear to be borne terminally on the fertile branches of the rachis; it is a striking fact that the seed-bearing frond or pinna should be so little modified as to show the same form of pinnule as the vegetative foliage; the differentiation of the sporophyll had scarcely even begun in a case like this.

The seed shown in Fig. 78 is incomplete at the top; more perfect specimens have a somewhat sharp point, more or less oblique at the apex; this probably marks the position of a micropylar tube (Fig. 84, A, p. 216; cf. *Trigonocarpus*, Fig. 79, p. 205).

The second case of continuity between a seed and the frond of a *Neuropteris* was recorded by Kidston and Jongmans in 1911,¹ in *N. obliqua*, a species allied to *N. heterophylla*. The specimen was derived from the Westphalian Coal-measures of Limburg, Holland. Here the seeds are borne in a pair on the ends of a forked rachis, which also bears the pinnules characteristic of the species. The seeds themselves are of the same type as those of *N. heterophylla*, but are considerably larger, measuring at least 4.5 cm. in length by 2.5 in maximum width.

A doubt has been suggested whether the bodies described as seeds in these species of *Neuropteris* may not merely have been large vegetative bands, such as occur among recent Ferns. The points of agreement with undoubted seeds, and especially the indications of a micropylar tube, seem, however, to be conclusive in favour of their seed-nature.

The names *Neuropterocarpus*, Grand'Eury, and *Neospermum*, P. Bertrand, have been proposed for the type of seed just described; such names may be required in cases where it is not possible to refer the seed to a definite species of frond. Some instances of association without continuity will be mentioned later.

¹ R. Kidston and W. J. Jongmans, "Sur la fructification de *Neuropteris obliqua*, Brongn.," *Archives néerlandaises des Sciences*, Ser. iii. B, tome i. p. 25, 1911.

Dr. Kidston was the first to observe direct continuity between the seed and the frond in a Fern-like Palaeozoic plant, and it was his discovery, in conjunction with the equally strong though less direct evidence in the case of *Lyginopteris*, which first suggested the institution of the class Pteridospermeae.

There is at present no instance of a petrified seed, showing structure, which can be referred to the Medulloseae or Neuropterideae with the same certainty as the casts just described. One of the best-known Palaeozoic seeds, however, *Trigonocarpus Parkinsoni*, Brongn., may be attributed with great probability, as we shall see, to *Alethopteris*; we will therefore shortly describe its structure.

Trigonocarpus Parkinsoni is found in three distinct states of preservation in the English Coal-measures: (1) in the common condition of nut-like, somewhat triangular casts which, as shown by Hooker and Binney and by Williamson, are really internal casts of the seed cavity; (2) as external casts, showing the testa and the true form of the seed; (3) as petrifications, in which the structure is more or less perfectly preserved. From these various data a fairly complete knowledge of the organisation of the seed has been gained; its more important features are shown in the diagrammatic figures 79-81.

The seed is a very large one, the length reaching 5 cm., of which quite half is accounted for by the enormously long micropyle; the body of the seed has a maximum diameter of over 2 cm. (Fig. 79). The testa consists of two clearly distinct layers—the outer layer or sarcotesta, composed of delicate, partly lacunar tissue, bounded externally by a sharply differentiated hypodermis and epidermis, and the inner ribbed sclerotesta, constructed, like the stone of a peach, of dense, thick-walled tissue. The ribs show a very definite arrangement. There are three principal ridges, corresponding

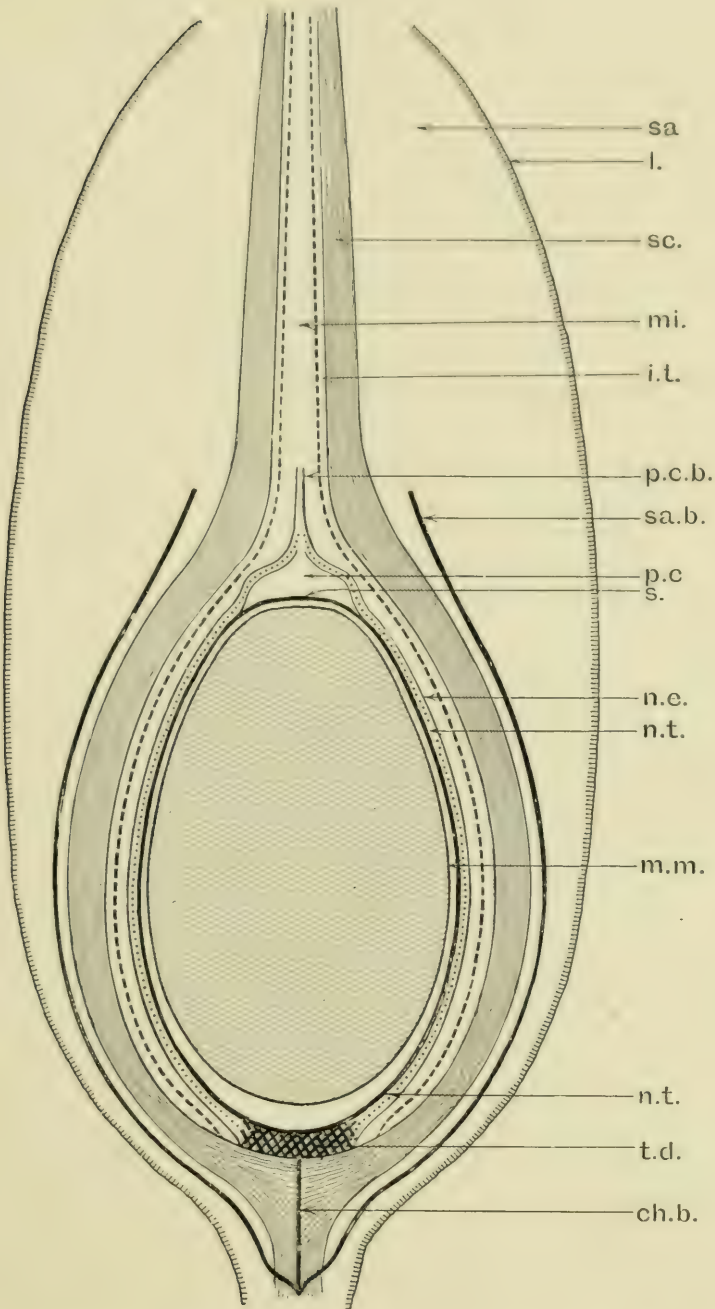


FIG. 79.—*Trigonocarpus Parkinsoni*. Diagrammatic median section in the plane of the "wing" (Fig. 81). *sa*, sarcotesta; *l*, its limiting layers; *sc*, sclerotesta; *mi*, micropyle; *i.t.*, remains of "inner flesh"; *sa.b.*, sarcotestal bundles; *p.c.*, pollen-chamber; *p.c.b.*, its beak; *s*, septum at bottom of pollen-chamber; *n.e.*, nucellar epidermis; *n.t.*, nucellar tracheal system; *m.m.*, membrane of megaspore; *t.d.*, tracheal disc at chalaza; *ch.b.*, chalazal bundle. \times about 3. From a drawing by Mr. A. J. Maslen, F.L.S.

to sutures, in the sclerotesta, and usually three secondary ridges in each space between the former, making twelve ribs in all (Fig. 80); within the sclerotesta there are some traces of an inner soft layer. The nucellus has a definite epidermis, and appears to have been free from the integument, from the chalaza upwards; it terminates at the apex in a dome-shaped pollen-chamber, provided with a long, narrow beak (Fig. 79, *p.c.*, *p.c.b.*), as in the

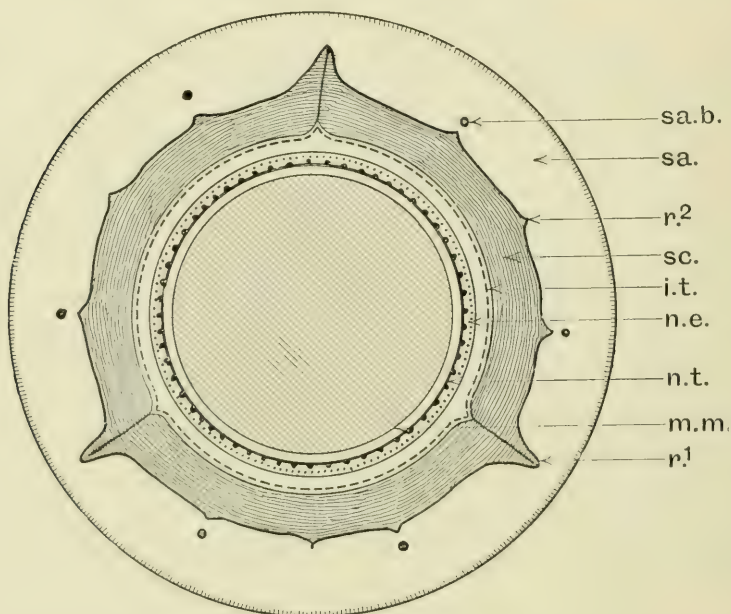


FIG. 80.—Diagrammatic transverse section through the body of the seed, at about the level of the line *m.m.* in Fig. 79. *r*¹, principal ridges; *r*², secondary ridges. Other lettering as in Fig. 79. × about 3. From a drawing by Mr. A. J. Maslen.

seeds of the Cordaiteae, described in Chap. IV. The membrane of the megaspore or embryo-sac is evident but the prothallus has not yet been found preserved.

The vascular system of the seed is double. At the base six bundles branch off from the common supply-strand and pass upwards through the sarcotesta (Fig. 79), taking a definite position opposite certain of the secondary ridges (Fig. 80). These bundles appear to have been collateral, with external phloem, and there is evidence that the xylem was mesarch. The inner

vascular zone formed a complex tracheal network in the nucellus; near the chalaza the sheath of nucellar tracheides is continuous; farther up they range themselves in longitudinal strands connected by abundant transverse anastomoses. The most remarkable feature of the seed is the long micropylar tube, formed by an extension of the ribbed sclerotesta, and enclosed in a broad, wing-like prolongation of the sarcotesta (Figs. 79, 81). It is not quite certain, however, to what extent the flattened form of this part of the seed is natural.

The seed, with its fleshy and stony coats, double vascular system, and pollen-chamber, is evidently very

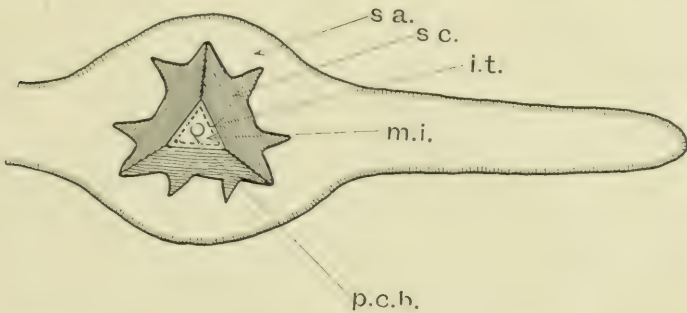


FIG. 81.—Diagrammatic transverse section through the micropyle, at about the level of the line *p.c.b.* in Fig. 79, showing the wing on one side. Lettering as in Fig. 79. From a drawing by Mr. A. J. Maslen.

nearly akin to the seed of a recent Cycad, the chief difference consisting in the free nucellus, whereas in the modern family it is adherent to the integument.

The petrified specimens of *Trigonocarpus Parkinsoni* are, almost without exception, associated with the leaflets, petioles, and other organs of *Medullosa anglica*, while the casts very generally occur together with the *Alethopteris* foliage, which no doubt belonged to that plant and allied species of *Medullosa*. Histologically there is a striking agreement in the tracheides, a peculiar, finely scalariform type being characteristic both of the *Medullosa* and the *Trigonocarpus*. There is also a certain similarity between the limiting layers of the sarcotesta

and those of the petiole. The evidence is of course far from amounting to proof, but the presumption is entirely in favour of this seed being the fructification of the *Alethopteris* (probably *A. lonchitica*), which formed the foliage of *Medullosa anglica*.¹

The structure of another species of *Trigonocarpus* (*T. shorensis*, from the Lower Coal-measures of Shore, Littleborough) has been fully investigated by Dr. Salisbury.² This is a large seed, over 4 cm. in length by nearly 2.5 cm. in maximum breadth, and of a stouter build than *T. Parkinsoni*. The micropylar beak is short; there are three principal ribs on the hard shell; the secondary ribs die out below the middle of the seed, and tertiary ribs are absent. The sclerotesta is thinner and the sarcotesta thicker than in *T. Parkinsoni*; there is a well-marked transition from one to the other, indicating that they were derived from a single integument. The bulk of the sarcotesta has a lacunar structure, but the external layers are somewhat complex, including a system of radial sclerotic plates, comparable to the hypoderma of a *Medullosa*, accompanied by numerous secretory elements. The six mesarch vascular bundles of the sarcotesta are distributed round its outer border. The internal vascular system forms a tracheal cup at the base of the nucellus, with numerous mesarch strands lining its inner surface. The epidermis of the nucellus, which is free from the testa, is even more pronounced than in *T. Parkinsoni*. Thus the two seeds show a general agreement in their construction, while differing in a number of definite specific characters.

¹ On *Trigonocarpus* see Hooker and Binney, "On the Structure of a certain Limestone Nodules enclosed in seams of bituminous Coal, with a description of some Trigonocarpons contained in them," *Phil. Trans. Royal Soc.* vol. cxlv. 1855. Williamson, "On the Organisation of the Fossil Plants of the Coal-measures," Part viii. *ibid.* vol. clxvii. 1877. Scott and Maslen, "The Structure of *Trigonocarpus*," *Ann. of Bot.* vol. xxi. 1907.

² E. J. Salisbury, "On the Structure and Relationships of *Trigonocarpus shorensis*, sp. nov.," *Ann. of Bot.* vol. xxviii. 1914, p. 39.

No pollen-grains have yet been observed in the pollen-chamber of *Trigonocarpus*,¹ but in another genus of the same group, *Stephanospermum*, Brongn., reinvestigated by Prof. F. W. Oliver, they have been found in perfect preservation. The species to which Figs. 82 and 83 refer, *Stephanospermum akenioides*, Brongn., is one of the numerous seeds, originally described by Brongniart, from the Black Pebbles of St. Croix, near St. Étienne, of Upper Coal-measure age. It is a comparatively small seed (measuring about 10×4.5 mm.), and, though the sarcotesta is not preserved, is evidently of the same general type as *Trigonocarpus*, with which it agrees in the radial symmetry, the prolonged micropyle, the beaked pollen-chamber, and the apparently free nucellus, of which the characteristic tracheal investment forms part.

The most striking peculiarities of the seed consist in the presence of a prominent ring or collar of the sclerotesta around the micropylar region, and in the nature of the nucellar tracheal system, which forms a continuous mantle of spiral or scalariform tracheides, extending as far as the pollen-chamber and spreading over its floor.

In this seed the prothallus is sometimes well preserved; the archegonia appear to have been only two in number; in the egg-cell the nucleus has been recognised.

The apex of the pollen-chamber was prolonged into a long beak or tube, engaging with the micropyle (cf. Fig. 79, *Trigonocarpus*).² Through this beak the pollen-grains entered the pollen-chamber, in which they are found in almost every seed. They also occur loose in the matrix, where they are of small size, averaging only about 60μ in length, while the average dimensions of those in the pollen-chamber are $160 \times 100 \mu$ (210μ being the extreme length observed), so that, as Renault first

¹ Except in a minute seed, *T. pusillus*, Brongn. referred to that genus.

² In Fig. 82 the conical mass at the top of the figure represents the funnel-shaped base of the tube, but the tube itself is missed.

showed, the pollen-grains developed actively after entering the seed. The multicellular structure of the pollen-grains, in this and other cases, was first demonstrated by Renault, and fully confirmed by the more recent observations of Oliver, who finds that there are about twenty cells in each grain, so arranged that five radial septa are seen when the grain is cut transversely (Fig. 83). Ultimately the internal cells appear to have become retracted towards the periphery, leaving behind

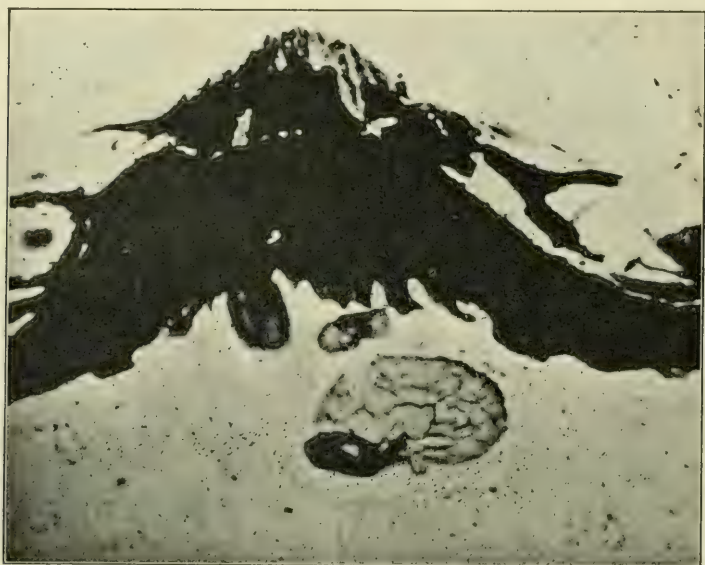


FIG. 82.—*Stephanospermum akenioides*. Upper part of pollen-chamber, showing part of its wall, with the base of the beak. In the chamber a large multicellular pollen-grain is shown, also three small foreign pollen-grains, one of which partly overlies the large grain. $\times 90$. Will. Coll. 1486a. From a photograph lent by Prof. F. W. Oliver, F.R.S.

them in the middle of the grain a framework of cell-wall—the “replum” (see Fig. 83).

In the light of our present knowledge of the reproduction of *Ginkgo* and the Cycads, it is an obvious suggestion that the internal cells of the pollen-grain were antheridial cells, producing spermatozoids. Renault, however, actually anticipated the discovery of Ikeno and Hirase. In an allied seed, *Aetheotesta*, as well as in *Stephanospermum* itself, the cell-walls of the pollen-grains which they contain are perforated, and Renault

suggested, in 1887, "that the perforations served for the passage of mobile bodies analogous to antherozoids." He adds: "We do not regard as impossible the existence in the past of pollen-grains, which, instead of effecting fertilisation by means of a tube, discharged into the pollen-chamber of the appropriate seeds antherozoids capable of performing this function."¹

Renault's prescience has been fully justified by subsequent discoveries²; possibly even the direct proof of



FIG. 83.—*Stephanospermum akenioides*. Multicellular pollen-grains in pollen-chamber; some shreds of the wall extend into the cavity. The middle pollen-grain is in transverse section, and shows the radiating septa dividing up the grain. The grain to the right is in longitudinal section, and shows the peripheral cells and the "replum" in the middle (see text). $\times 137$. Univ. College Coll. S 7A. From a photograph lent by Prof. Oliver.

the existence of spermatozoids in fossil Seed-plants may yet be obtained.²

The presence of a pollen-tube in the case of *Stephanospermum* and other Palaeozoic Spermatophytes is very doubtful. Small papillae are occasionally observed (as

¹ Renault, "Note sur le genre *Aetheotesta*," *Mém. de Soc. d'Hist. nat. de Saône-et-Loire*, pp. 156, 158, 1887. For *Stephanospermum* see Brongniart, *Graines fossiles silicifiées*, 1881; Renault, *Cours de bot. fossile*, t. iv. p. 184, Plates xxi. and xxii. 1885; F. W. Oliver, "Structure and Affinities of *Stephanospermum*," *Trans. Linn. Soc. London*, 2nd ser. Bot. vol. vi. Part viii. 1904.

² Evidence on this subject is adduced in Prof. F. W. Oliver's memoir "On *Physostoma elegans*," *Ann. of Bot.*, January 1909.

in the large pollen-grain shown in Fig. 82), but their significance is still uncertain. Some further reference to the question will be made in discussing the fertilisation of the Cordaiteae (Chap. IV. p. 300).

It is only in the cases of *Neuropteris heterophylla* and *obliqua* that we have, as yet, the direct proof that Neuropterideae bore seeds; as we have seen, there is strong, though less conclusive, evidence that the seed *Trigonocarpus Parkinsoni* belonged to *Medullosa anglica*, which, according to its foliage, was certainly an *Alethopteris*.

A considerable mass of evidence, mainly from association, has further been accumulated through the extensive investigations of M. Grand'Eury and others, both in the Upper Coal-measures of Central France and in the more ancient deposits of Belgium, Northern France, and the Saar Valley. Grand'Eury, whose experience in such researches was unrivalled, found that the vegetative organs of Neuropterideae, wherever there was evidence that they grew *in situ*, were constantly associated with seeds of the radially symmetrical type, such as rarely occur in company with plants of any other group; he further found special types of seed in close association with definite genera and species of frond. Considering the wide field covered by Grand'Eury's observations, and the fact, which he established, of the social growth of plants of the same group, there can be no doubt of the value of the conclusions arrived at. Grand'Eury was led to refer some fifteen genera or sub-genera of seeds to the Neuropterideae, the general characters of the seeds being that they are of radial symmetry and striated, polygonal, or winged, the number of the angles or wings being some multiple of three.

Among Grand'Eury's special results we may mention that he referred the huge seed *Pachytesta gigantea* (sometimes 4 inches long) to a species of *Alethopteris* (*A. Grandini*), and smaller seeds of the same type to other species of the genus. In the Northern Coal-fields, how-

ever, he found *Trigonocarpus* seeds associated with certain Alethopterids (in agreement with our conclusion as to *T. Parkinsoni*), and pointed out the affinity between *Pachytesta* and *Trigonocarpus*.

A considerable variety of seeds has been referred to *Neuropteris*; the seed attributed to *N. flexuosa* appears to be of the same type as that of *N. heterophylla*, discovered by Kidston.

Various seeds have also been referred (not to mention other cases) to the genera *Odontopteris* and *Linopteris* (= *Dictyopteris*), which are some of those which Stur had already removed from the Ferns in 1883.

Grand'Eury in several cases detected the "inflorescence" or fertile rachis on which the seeds were borne. He was of the opinion that, as a rule, the organs of reproduction of Neuropterideae and other Pteridosperms were borne on "special organs, separate from the leaves, *i.e.* on independent inflorescences." In *Neuropteris heterophylla*, however, and in other cases, to be subsequently mentioned, the seeds were borne on a frond but slightly modified, so there can be little doubt that the organ supporting them, even when more specialised, was still foliar in nature.¹

Some further cases of the association of seeds with the foliage of various Neuropterideae have come to light more recently. A ribbed seed ("*Rhabdocarpus*, cf. *tunicatus*") has been found both by Dr. Renier and Dr. P. Bertrand, in close association with the fronds of *Neuropteris Schlehani*, another species of the same group as *N. heterophylla*. The specimens occur in the Coal-measures of Belgium and Northern France.

Another type of seed, *Hexapterospermum*, Brongn., occurs in similar localities, associated with *Neuropteris*

¹ C. Grand'Eury, "Sur les graines des Neuroptéridées," *Comptes rendus*, t. 139, pp. 23 and 782, 1904; "Sur les inflorescences des fougères à graines du Culm et du terrain houiller," *Comptes rendus*, t. 143, p. 761, 1906.

gigantea, a species representing a different group from that of *N. heterophylla*. These seeds have a six-angled sclerotesta, enclosed in what was probably a fleshy outer coat; they thus bear some resemblance to *Trigonocarpus*. Cup-like, fringed bodies, also associated with the seeds, have been interpreted as their cupules, but the evidence for the presence of a cupule in Neuropterideae is by no means conclusive.

Another species of *Hexapterospermum* is associated with fronds of *Linopteris obliqua*; in this case no "cupules" have been met with. *Linopteris* is a genus closely allied to *Neuropteris*, from which it chiefly differs in the reticulate venation of the pinnules.

We thus see that while the direct proof of continuity between seed and frond is still limited to two species of *Neuropteris*, there is a considerable body of indirect evidence which, as far as it goes, supports the opinion that the Neuropterideae generally were seed-bearing plants.

We have still but little positive knowledge as to the nature of the male organs in the Neuropterideae. In 1887 Dr. Kidston described a form of fructification in *Neuropteris heterophylla*, the species in which he subsequently discovered the seed. The specimen¹ consists of a forked rachis, bearing the normal vegetative pinnules below, while the branches terminate in small four-lobed bodies, which may be interpreted either as groups of sporangia or as cupules (Fig. 84, B). As there is no evidence for the presence of minute cupules of this kind in Neuropterideae, the former interpretation is somewhat the more probable, in which case the specimen would no doubt represent the microsporangiate fructification. M. Grand'Eury also observed a rachis bearing sporangium-like bodies in *Neuropteris*, and "floral discs," which he regarded as male, in *Linopteris*.

¹ The figure and description are reproduced in Dr. Kidston's paper on "The Fructification of *Neuropteris heterophylla*," above cited.

In later years our information has somewhat increased, and here again the most definite advance is due to Dr. Kidston.

A peculiar form of leaflet, apparently bearing sporangia (cf. Fig. 84, C), had been observed both by the Abbé Carpentier and Dr. P. Bertrand,¹ in association with *Neuropteris gigantea* and similar species. The leaflets are more or less orbicular, and large, reaching half an inch or more in diameter. They appear to have been of a fleshy consistency and are traversed by radiating and forking veins. They resemble the "cyclopteroid" pinnales which occur on the fronds of *Neuropteris gigantea* (see p. 172). The sporangia were found by Carpentier to be embedded in the substance of the thick lamina.

Dr. Kidston has discovered similar pinnules in the Westphalian of Coseley, near Dudley. They are borne terminally on the branches of a stout rachis. The under side of the rounded pinnules bears densely packed, narrow, elongated sporangia, from which Dr. Kidston obtained numerous spores by maceration; they are from 45 to 60 μ in diameter and show a tri-radiate ridge. Thus, the sporangia were no doubt the pollen-sacs of the plant. Further, Dr. Kidston found on the same rachis, sterile pinnules, which are clearly those of a *Neuropteris*, though the species could not be identified. The provisional name *Neuropteris Carpentieri*, Kidston, is therefore used for these specimens. As Dr. Kidston says, "that the fossils just described are the microsporangial organs of a *Neuropteris* can scarcely be doubted."

Somewhat similar fertile pinnae were described by Zeiller under the name *Potoniea adiantiformis* (Fig. 84, C), and the French specimens described by Carpentier and P. Bertrand have also been referred to the pro-

¹ See the memoirs by Carpentier cited on p. 76. Also P. Bertrand, "Les Fructifications de Neuroptéridées," *Ann. de la Soc. Géol. du Nord*, t. xlii. p. 113, 1913.

visional genus *Potoniea*, and even to the same species, but, as Kidston has pointed out, they differ in certain respects from Zeiller's specimens,¹ which, however, probably belonged to the same group.

Two types of supposed male organs have been attributed to the genus *Linopteris*, but only on the evidence of association. A fructification much resembling a large

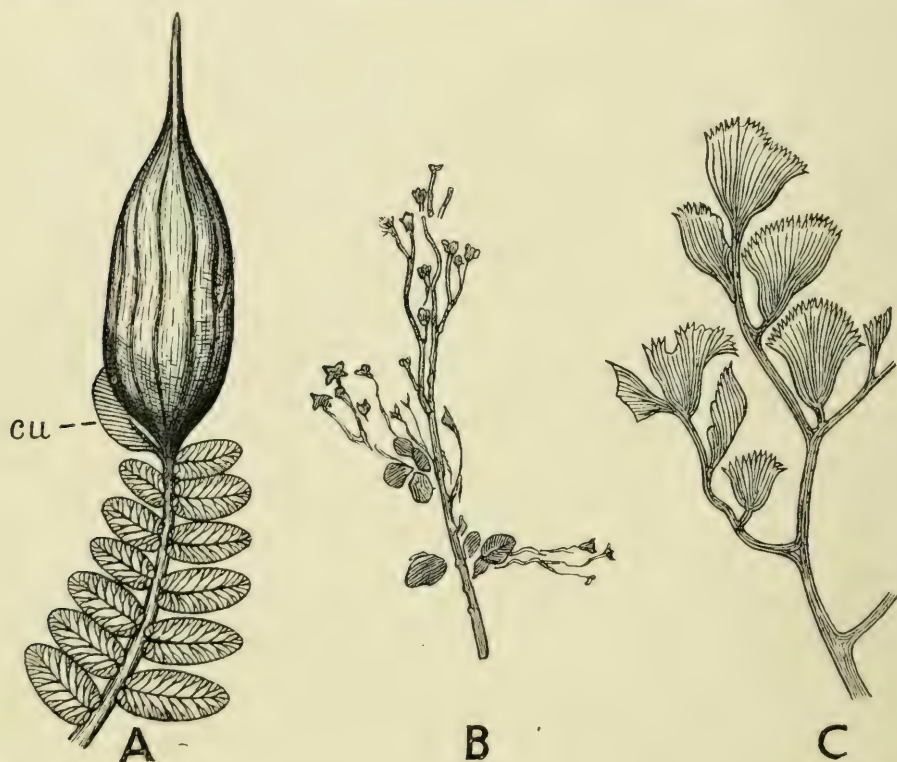


FIG. 84.—Neuropterid Fructifications. A. Restoration of a seed-bearing pinna of *N. heterophylla*, showing the micropylar beak of the seed; *cu*, supposed cupule. After P. Bertrand. B. Fructification (probably ♂) of *N. heterophylla*. After Kidston. C. *Potoniea adiantiformis*. ♂ Fructification of a Neuropterid. The teeth on the pinnules are believed to represent microsporangia. After P. Bertrand. All the figures are reduced.

Crossothea (see p. 75, Fig. 39) from the Upper Coal-measures of Commentry and Autun, was referred by M. Zeiller to the species *L. Germari*; the case for this attribution is a strong one, though continuity is lacking. There is, however, some doubt whether the fringe,

¹ R. Kidston, "On the Fossil Flora of the Staffordshire Coal Fields," Part iii., *Trans. Royal Soc. of Edinburgh*, vol. 1. Part i. 1914, p. 112.

which in true *Crossothecas* consists of microsporangia, may not in this case represent mere expansions of the pinnule, perhaps concealing the actual reproductive organs. Our knowledge of the fructification cannot therefore be regarded as satisfactory.

On the other hand, the "floral discs" attributed to *L. Brongniarti* and *L. obliqua* are of the "*Potonia*" type, though more peltate and cupulate than the fertile pinnules referred to *Neuropteris gigantea*. While the evidence from exclusive association and resemblance to sterile pinnules strongly supports the attribution of the bodies in question to *Linopteris*, little or nothing is known of the actual pollen-sacs which they may be assumed to have borne.

It may be pointed out that the fertile pinnules which appear to have borne the microsporangia in the cases last described are extremely different from the supposed male fructification of *N. heterophylla* (Fig. 84, B and C). Our knowledge, in fact, of these pollen-bearing organs in the whole group is still very imperfect; the clearest case is that of *N. Carpentieri*, described by Dr. Kidston. It is unnecessary to describe other fructifications, the attribution of which to Neuropterideae is merely a matter of conjecture.

M. Grand'Eury found evidence that various Neuropterideae possessed stolons and other means of vegetative propagation.¹

AFFINITIES OF MEDULLOSEAE

We may provisionally treat the family names Medulloseae and Neuropterideae as synonymous, for though there can as yet be no strict proof that the groups indicated were coextensive, yet there is evidence that the

¹ C. Grand'Eury, "Sur les organes et le mode de végétation des Neuroptéridées, et autres Ptéridospermes," *Comptes rendus*, t. 146, p. 1241, 1908.

Medullosean type of structure existed in several of the genera with Neuropteridean characters in the frond.

In the Medulloseae, as in the Lyginopterideae, we find certain not unimportant structural characters, even apart from the habit, which suggest an analogy with the Ferns. So far as *Medullosa* itself is concerned, the most Fern-like feature is the vascular system of the stem, which in its primary "polystelic" arrangement recalls the higher Ferns, and was compared by Weber and Sterzel in 1896 with that of *Psaronius*. The fact that this original ground-plan becomes more or less obscured as secondary growth goes on does not affect the nature of the primary structure, but a more decisive difference from the Ferns consists in the absence of leaf-gaps in *Medullosa* (see above, p. 188). The discovery of the *Sutcliffia* type of vascular system, which may be described as a modified protostele, renders it probable that polystely arose within the family Medulloseae, and we must certainly regard this character as a parallel development to the polystely of the Ferns and in no way as an inheritance from them. In *Sutcliffia*, however, the anatomy of the stem, peculiar as it is, might be compared, though remotely, with that of a protostelic Fern, while the concentric foliar bundles suggest some analogy. There is nothing to indicate any real relation between Ferns or other Pteridophyta and the Medulloseae, and the great complexity of the seed shows clearly enough how remote any connection with a cryptogamic phylum must have been. On anatomical grounds it seems not unlikely that this family may have had a common origin with the Lyginopterideae from some unknown protostelic type.

On the whole, the Medulloseae or Neuropterideae strike one as a more advanced group than the Lyginopterideae. Their seeds, if we may take *Trigonocarpus* as a type, perhaps approach nearer than any other Palaeozoic seeds to those of recent Cycadaceae, as shown

by the differentiation of the integument into a sarcotesta and a sclerotesta, the double vascular system and the form of the pollen-chamber ; the chief difference lies in the apparently free nucellus of the fossil seeds, a feature with which other distinctions may be correlated. As regards anatomical characters, the petiole and rachis of *Medullosa* very closely resemble those of a Cycad in structure ; the same may be said of the root. The stem-structure, however, throughout the Medulloseae is essentially different, for neither in the almost protostelic *Sutcliffia*, nor in the more complex polystelic stems of *Medullosa*, do we find, as it seems to me, any fundamental agreement with the stem either of recent Cycadaceae or of Mesozoic Bennettiteae, though certain analogies can be traced. On the whole of the evidence an affinity between the Medulloseae and the Cycadophyta of later periods appears well established, but we cannot assume that the former were the direct ancestors of the latter.

Dr. Ethel de Fraine, in her paper on *Sutcliffia*, framed an interesting hypothesis, which she stated as follows : " From such a type as *Sutcliffia*, which may be regarded as the most primitive member of the Medulloseae at present known, it is suggested that two divergent lines may have arisen. The one advanced with increasing complexity in the direction of multiplication of the number of steles, through some such form as *Medullosa anglica*, and ended blindly in the more complex Medulloseae. . . . The other maintained the protostelic condition, and advanced by further modification of the single vascular cylinder, and perhaps by the elaboration of the extra-fascicular arcs and accessory vascular strands of the cortex, in the direction of the Cycadales." ¹

This is a perfectly tenable view, which reconciles the affinity between Medulloseae and Cycads, with the essentially monostelic stem-structure of the latter. Connecting links are of course wanting at present, and the

¹ E. de Fraine, *l.c.* p. 1062.

suggestion therefore remains a pure hypothesis until further evidence becomes available. We shall return to the question in the final chapter.

ANEIMITEAE

The genus *Aneimites*,¹ Dawson, may be mentioned in connection with the Neuropterideae, to which it has sometimes been referred on foliar characters, though, as we shall see, the fructification shows that there can have been no near affinity. The habit of the fronds is like that of a Maiden-hair Fern (*Adiantum*), as the original generic name *Adiantites* implied; the genus extends from the Devonian to the Middle Coal-measures, and is characteristic of the Lower Carboniferous. In a species (*Aneimites* ² *fertilis*) from the Pottsville beds of West Virginia, of an age corresponding to that of our Millstone Grit, Dr. David White has demonstrated the presence of seeds on the fronds. They are borne on the apices of branched, terminal extensions of the peripheral pinnae; the pinnules on the adjacent sterile portions of the frond, though considerably reduced, retain the characteristic cuneiform shape. The small seeds (averaging 4.5 mm. in length) are rhomboidal in form, lenticular in cross-section, and winged; it thus appears that they were of the platyspermic (bilaterally symmetrical) type, which was once supposed to characterise the Cordaiteae. As the specimens are only known in a carbonised condition, nothing certain can be said as to the structure, though the discoverer believed that he detected indications of the micropyle and pollen-chamber. The isolated seeds were named *Wardia fertilis*

¹ David White, "The Seeds of *Aneimites*," *Smithsonian Miscellaneous Collection*, vol. xxvii. p. 322, 1904.

² The older and more familiar name, *Adiantites*, Göppert, is maintained by some authors. *Aneimites* is still used here, because the seeds were originally described under that name.

before their connection with the frond was observed, and this name is retained by Prof. Seward. Dr. White has discovered different forms of the *Wardia* seeds in the most intimate association with four other species of the genus; in one of these, *A. tenuifolius*, Göppert, they again occur in actual connection with the frond. The author points out that the proof of the Pteridospermous nature of *Aneimites* throws suspicion on various similar frond-genera, in one of which, *Eremopteris*, there appears to be strong evidence from other sources for the occurrence of seeds of a platyspermic type. The specimens of the Coal-measure species, *E. artemisiaefolia* (Sternberg), are almost constantly associated with the platyspermic seed, *Samaropsis acuta* (L. and H.). The seeds of *Aneimites* resemble some of those grouped under the name *Cardiocarpon*, and it may be hoped that this clue may eventually lead to the recognition of their structure.

SEED-BEARING PECOPTERIDEAE

Up to the year 1905 the form-genus *Pecopteris* was regarded as the stronghold of the true Ferns, no suspicion of other alliances attaching to any of its members. In that year, however, M. Grand'Eury made the striking discovery that the species *Pecopteris Pluckenetii*, from the Upper Coal-measures of St. Étienne, was a seed-bearing plant.¹ In twenty specimens he found the seeds attached by hundreds to the fronds. Sometimes they occur on pinnae of the usual vegetative form, but where they are numerous the lamina is somewhat reduced. The seeds are attached at the ends of the stout lateral veins of the pinnules (see Fig. 85). They are described as forming a wide angle, when in the natural condition, with the plane of the lamina, so that they no doubt hung down freely from the under side of the fertile

¹ "Sur les graines trouvées attachées au *Pecopteris Pluckenetii*, Schlot.," *Comptes rendus*, t. cxl. p. 920, 1905.

frond. The seeds, like those of *Aneimites*, are winged (Fig. 85), and resemble *Samaropsis*, a seed of which other species have been assigned to the Gymnosperm *Dory-*

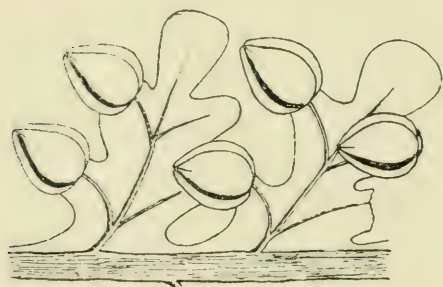


FIG. 85.—*Pecopteris Pluckeneti*. Fragment of a fertile pinna with seeds attached near the ends of the lobes. $\times 3$. From Zeiller, after one of Grand'Eury's specimens.

cordaites (see p. 267) so closely that the two may easily be confused when found isolated.

The species *P. Pluckeneti* belongs to a section of the genus characterised, according to Prof. Zeiller, by the large, lobed pinnules, and the dichotomously branched frond, with a bud, capable of further

growth, in the axil of each bifurcation.¹ Though usually included in *Pecopteris*, some authors have placed the species in other genera, and notably Sterzel, in 1883, founded a new genus, *Dicksoniites*, for its reception, because he observed, in some specimens, round disks at the margins of the pinnules, which he compared to the sori of *Dicksonia*.² The nature of these bodies appeared to have been elucidated by a later observation of M. Grand'Eury's. He stated that he found "stellate groups of anthers in the place of the receptacles," and that they were borne on different specimens from those showing seeds.³ But there is also evidence suggesting that the "receptacles" may represent the scars of seeds which had been shed.

There is another species of *Pecopteris*, *P. Sterzeli*, Zeiller, which so closely resembles *P. Pluckeneti*, in the form and mode of branching of the frond, that Prof. Zeiller had no doubt that this too was a Pteridosperm,

¹ Zeiller, *Éléments de paléobotanique*, p. 89, 1900.

² "Über *Dicksoniites Pluckeneti*," *Bot. Centralblatt*, Bd. xiii. 1883.

³ See Grand'Eury, "Sur les inflorescences des fougères à graines," etc., *Comptes rendus*, t. cxliii. p. 764, 1906.

though the seeds have not yet been observed. There is evidence of considerable weight that the fronds of *P. Sterzeli* were borne on a *Caulopteris* stem—*Caulopteris*, as already stated, representing the casts of “Tree-fern” stems, the structure which, when known, is that of *Psaronius* (Vol. I. p. 268). Although Prof. Zeiller ceased to regard the connection between *Pecopteris Sterzeli* and the *Caulopteris* as proved, it seems desirable to call attention to the question. If the attribution should be confirmed by future investigation,¹ the relation of the Marattiaceous to the Pteridospermous Pecopterids will need serious reconsideration.

It has already been mentioned (Vol. I. p. 262) that additional evidence for the Pteridospermous nature of certain Pecopterids is afforded by the fact that they bore fructifications of the *Crossotheca* type. Dr. Kidston² enumerates three species of *Crossotheca* in which the foliage is known to have been that of a *Pecopteris*, and there are two other species in which this was probably the case. As Dr. Kidston says: “Having shown that the supposed sporangia of one species of the genus [*Crossotheca*] are in reality the microsporangia of one of the Pteridosperms, I think we are justified in provisionally concluding that all the remaining species also belong to the Pteridospermeae, even though we do not possess a complete knowledge of the structure of their microsporangia.” There is thus a presumption that a considerable fraction of the old genus *Pecopteris* is made up of seed-bearing plants.

One of the probable Pecopterid Crossothecas, *Pecopteris exigua*, Ren.,³ from the Permo-Carboniferous of Autun, occurs in the silicified condition, with structure preserved,

¹ For the history of this question see Zeiller, *Flore fossile de Commeny*, Pt. i. 1888, p. 184, Plate viii.; *Bassin houiller et permien de Blanzy, flore fossile*, 1906, p. 62.

² *Microsporangia of the Pteridospermeae*, p. 432.

³ Renault, *Cours de bot. fossile*, année 3, p. 115, Plate xix. Figs. 13-18, 1883.

but only fertile portions of the frond appear to be known. The little fertile pinnules, elliptical in form and about 1 mm. long, are inserted on the rachis like the leaflets of a *Pecopteris*. Each pinnule bears, on its lower surface, two rows of ovoid, pointed sporangia, three or four in each row; they appear to be free from each other, and do not show the bilocular structure described by Dr. Kidston in the *Crossothea* of *Lyginopteris*. There is, of course, no proof that they were microsporangia, but the general resemblance to a *Crossothea* tells in favour of this supposition.

In *Callipteris*, a characteristic Permian genus of comparatively small bipinnate fronds, placed by M. Zeiller in Pecopterideae, M. Grand'Eury found evidence that seeds were present in at least two species. The seeds, which appear to have been borne on a slender, branched rachis, are of an elliptical or roundish shape, and from 5 to 10 mm. in length, and are described as resembling berries, and as the simplest in form of any Pteridospermous seeds. Bodies resembling an enormous *Crossothea*, 2 to 3 cm. in length, and bearing marginal sporangia, are regarded as possibly constituting the male organs of the plant. M. Grand'Eury pointed out that *Callipteris* differs widely from the Neuropterideae in its organs of reproduction as well as in foliar characters.¹

The common Coal-measure "Fern," *Mariopteris muricata*, with forked primary pinnae and a *Lygodium*-like habit, was found by M. Grand'Eury in close association, if not in connection, with small seeds,² so it is probable that this Pecopteroid form, in which no Fern-like fructification has ever been observed, will likewise prove to belong to the Pteridosperms. It has been suggested

¹ Grand'Eury, "Sur les graines et inflorescences des *Callipteris*," *Comptes rendus*, t. cxliii. p. 664, 1906.

² Grand'Eury, "Sur les organes et le mode de végétation des Neuroptéridées et autres Ptéridospermes," *Comptes rendus*, t. cxlvi. p. 1243, 1908.

by Dr. Gothan that *Mariopteris* may have belonged to a Coal-measure *Heterangium*.

We see, then, that on present evidence there is every reason to believe that a large proportion of the Fern-like Palaeozoic plants with Pecopteroid foliage will find their place, like *Pecopteris Pluckencti*, among seed-bearing plants. As we have already seen (Chap. VIII. Vol. I.), there are still good grounds for the opinion that some other Pecopterids were true Ferns; much further investigation will be necessary before we are able to discriminate with certainty between the two classes of plants represented among fossils of this habit.

DOLEROPHYLLUM

Some remarkable fossils, described under this name, may be mentioned here; they would be of great interest, if it were certain that the various organs belonged to the same plant or to the same genus; as, however, this is not proved, a very brief notice must suffice.

The vegetative organs referred to *Dolerophyllum*, Saporta, consist of large, circular, peltate leaves, borne on an axis. In *D. Berthieri*, Ren., the leaves are 18 to 20 cm. in diameter; the numerous veins are forked. This species was derived from the Permo-carboniferous of France (Mont-Pelé, near Épinac). Other species have been described; *D. Goepperti*, Saporta, the first to be recorded, came from the Permian of the Ural in Russia, and is in the form of large buds, 3 inches long. The young, convolute leaves resemble the mature leaves of the French specimens, but the relation is uncertain. The anatomical structure is partly preserved; there are stomata on the upper surface of the leaves; the numerous vascular bundles appear to be of the collateral mesarch type, familiar in Cycadophyta.

Associated with the leaves of the Mont-Pelé species, Renault found some carbonised discs, containing pollen-

grains or spores, and attributed them to the *Dolerophyllum*. Petrified fragments of similar bodies were discovered at another locality (Grand Croix) and are probably of the same nature. The discs are 5-6 cm. in diameter with a thickness of 15-20 mm. The thick lamina is perforated by a number of vertical tubes, or immersed sporangia, filled with large pollen-grains or spores. Each grain measures about $460 \times 330\mu$; it appears to have opened by an operculum in the outer wall, and the interior is divided into 8 or 10 cells, thus resembling many other Palaeozoic pollen-grains.

The structure of the staminate discs, however, is unique, and throws no light on the affinities of the plant.

A seed, *Aetheotesta elliptica*, Ren., of the *Trigonocarpus* group, was attributed by Renault to *Dolerophyllum*, on the ground of a certain similarity between the pollen-grains found in its pollen-chamber and those of the staminate discs. The evidence, however, is quite indecisive.

The affinities of the genus, supposing that the scattered organs are rightly referred to one type of plant, are wholly uncertain. *Dolerophyllum*, if a natural group, probably belonged to some branch of the Pteridosperms, somewhat remote from the better-known families, but perhaps nearest to the Medulloseae.¹

COMPLEX STEMS OF UNCERTAIN AFFINITY

Steloxylon, Solms.—This genus was founded by Solms-Laubach on the *Medullosa Ludwigii* of Göppert and Stenzel, a fossil discovered near Semipalatinsk, in Western Siberia. It was found in a secondary deposit, and its geological age is therefore doubtful; it may be Permian or older. Dr. P. Bertrand states that one of the Saalfeld

¹ For *Dolerophyllum* see Renault, "Bassin houiller et permien d'Autun et Épinac," *Flore fossile*, ii. 1896, p. 260, Pl. lxxii.; Seward, *Fossil Plants*, vol. iii. 1917, p. 132.

specimens, attributed to *Cladoxylon dubium*, is really a *Steloxylon*; if this is the case, the genus goes back at least to the Lower Carboniferous.

The original specimen formed part of a fairly large stem, quite 5 inches in diameter. The structure differs from that of both *Medulloseae* and *Cladoxyleae*. The stem contains a great number of steles, some nearly circular in transverse section, others elongated. In the latter case, the longer diameter of the stele is radially directed, as in the *Cladoxyleae*. The steles are everywhere connected by anastomosis, forming a complex network. The exterior of the stem is clothed in an armour of crowded, rather small petiole bases, spirally arranged, and in this respect differs widely from either of the families above mentioned. Further, each leaf-base receives two or more branches from the external steles of the stem. The leaf-trace strands retain their stellar structure, and so far resemble the foliar strands of *Cladoxyleae* rather than those of *Medulloseae*.

Each stele, as preserved, consists mainly of secondary wood; no doubt there was some primary xylem in the middle, but it was little developed, and nothing is known of its structure. The foliar steles, entering the leaf-bases, have the same, largely secondary, structure. The pitting of the tracheides is of the multiseriate, bordered type, as in the *Medulloseae*. Medullary rays are present; they widen out towards the centre of the stele.

The most important differences from *Medulloseae* are, first, the orientation of the steles, which are elongated radially and not tangentially; secondly, the structure of the leaf-bases, with a few steles, instead of numerous, relatively small bundles. From *Cladoxyleae*, *Steloxylon* differs in the pitting of the tracheides. The dense armour of small leaf-bases is a character equally foreign to both groups. In his note of 1914 Dr. Bertrand goes so far as to suggest that *Steloxylon* may simply represent a special condition of *Cladoxylon*, but the differences

just mentioned render this view difficult to accept. It is much to be desired that Dr. Bertrand's results, hitherto only briefly indicated in preliminary notes, may soon be published in full. In the meantime the position of *Steloxylon* remains uncertain; it is a polystelic stem, having some points in common both with the Medulloseae and the Cladoxyleae, but in other features very different from either.¹

Rhexoxylon, Bancroft. — The original species, *R. africanum*, was founded on a portion of a silicified stem from the Karroo series of South Africa. As this series of rocks ranges from Upper Carboniferous to Rhaetic or Lower Jurassic age, the antiquity of the specimen was uncertain, but the age was probably Triassic. The cortex and outer part of the vascular system are missing; the remaining central portion, about 7×5 cm. in diameter, shows an inner ring of "steles," with portions of an outer vascular zone. The "steles" consist in each case of a smaller external and a larger internal mass of secondary wood; the chink between the two was supposed to contain the original primary xylem. The surrounding phloem is still preserved. The outer vascular ring consists of normally orientated masses of secondary wood; they have been called "partial steles," but in this region there was never any evidence of stelar structure. The large stem-pith contains an irregular vascular plate or elongated stele, as well as some sclerotic nests and a few bands of periderm. The secondary wood of the various vascular masses has a dense structure like that of a Conifer, and is traversed by uniseriate medullary rays. The tracheides bear from one to three (usually two) rows of bordered pits on their radial walls, and have an Araucarian character.

¹ For *Steloxylon* see especially Solms-Laubach: "Über die in den Kalksteinen des Kulms . . . Pflanzenreste, iv. *Völkelia*, *Steloxylon*," *Zeitschrift f. Botanik*, ii. 1910; also the earlier literature there cited; also the note by P. Bertrand, cited above, on p. 158.

Rhexoxylon has recently been re-investigated by Mr. John Walton of Cambridge, whose results will shortly be published. He has had various important new specimens at his disposal, and recognises more than one species. He shows that no primary wood is present in the supposed "steles." Hence the structure is not polystelic, for all the anomalies are secondary. The affinity, once suggested, with Medulloseae must therefore be given up. Mr. Walton interprets the very remarkable structure as that of a climber or liane, of *Dadoxylon* type.¹

CYCADOXYLEAE

We have now to consider a series of fossil forms of which our knowledge is still imperfect, but which are of great interest, as they appear to connect the Lyginopterideae with a more distinctly Cycad-like type of structure.

A portion of a large stem, *Cycadoxylon robustum*, regarded by Williamson as belonging to his *Lyginodendron*, and subsequently named *L. robustum* by Prof. Seward, was discovered by Nield more than forty years ago, in the Lower Coal-measures of the Oldham district. Although the specimens are fragmentary, they show some points of considerable interest. No cortical tissues are preserved, and even the wood is probably incomplete, but the remaining, central part of the stem has a diameter of about 14 cm., so, in the natural condition, the plant must have reached the dimensions of a small tree. The secondary wood, which, in its present state, has a thickness of nearly 6 cm., resembles that of *Lyginopteris oldhamia* (Fig. 86, α^2). The medullary rays are broad, and of great height, so that the whole

¹ For *Rhexoxylon* see N: Bancroft, "*Rhexoxylon africanum*, a new Medullosean stem," *Trans. Linn. Soc. Botany*, vol. viii. 1913; Seward, *Fossil Plants*, vol. iii. 1917, p. 146. See also Mr. Walton's paper, when published.

character of the wood was very parenchymatous, like that of the recent Cycads. The tracheides, which have a somewhat sinuous course, bear multiseriate bordered pits on their radial walls.

The pith, which is almost 3 cm. in diameter, is imperfectly preserved, but there are distinct remains of

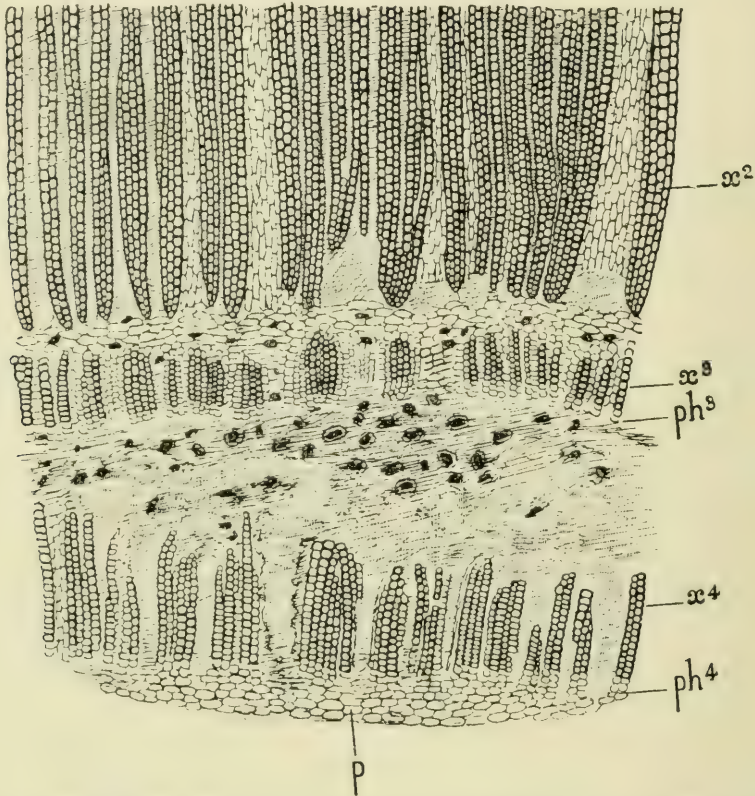


FIG. 86.—*Cycadoxylon robustum*. Part of transverse section, showing inner portion of normal wood, with two anomalous zones of wood and bast. x^2 , normal secondary wood; x^3 , ph^3 , first inverted band of medullary xylem and phloem; x^4 , ph^4 , second band of the same; p , pith. $\times 12$. S. Coll. 457. (G. T. G.)

scattered, dark groups of sclerotic tissue, such as we find in the pith of *L. oldhamia*.

The most characteristic feature of *Lyginopteris*, however, namely the strands of primary wood on the border of the pith, cannot be recognised with certainty in Nield's specimen, and if present, must, it would seem, have been much reduced. The remains of leaf-traces, passing out through the secondary wood, are seen at several

places, but even here the primary xylem of the outgoing bundle has not been detected. It must therefore remain an open question whether the primary structure of the xylem was of the *Lyginopteris* type, or whether the whole wood developed centrifugally, as in the stem of recent Cycads or Conifers. On the other hand, the large stem presents a peculiarity of structure which occurs in some specimens of *Lyginopteris oldhamia*. It was mentioned above (p. 40) that, in that plant, anomalous vascular tissues are sometimes developed in the outer part of the pith, immediately within the normal ring of bundles. These tissues, when present, have inverted orientation, the xylem facing outwards, towards the normal wood, and the phloem inwards, towards the centre of the pith. Precisely the same anomaly reappears, in a more striking form, in *Cycadoxylon robustum*. There is a distinct zone of secondary wood at the margin of the pith, reaching in places a thickness of about sixteen tracheides in a radial row, and on the inner side of the anomalous zone a corresponding band of phloem can be recognised (Fig. 86, x^3 , ph^3). Thus, the medullary vascular tissues had the same reversed orientation as in the corresponding anomalous formations sometimes found in *Lyginopteris oldhamia*. In *Cycadoxylon robustum* the anomalous vascular zone is at some places double, the second band of medullary wood and bast having the same orientation as the first (see Fig. 86, x^4 , ph^4).

The structure as a whole leaves little doubt that the fossil *Cycadoxylon robustum* really possessed some affinity with *Lyginopteris*, but, as there is no proof that the primary structure of the two was similar, we no longer place them in the same family, but have transferred the species discovered by Nield to the type-genus of the Cycadoxyleae, to which, as we shall now see, it naturally belongs.¹

¹ On *Cycadoxylon robustum* see Williamson, "Organisation of the Fossil Plants of the Coal-measures," Part iv. *Phil. Trans.* 1873,

The interest of the fossil depends on two points. The first is the thoroughly Cycadean character of the secondary wood, a character shown much more evidently in this large stem, which in its dimensions is comparable to that of a recent Cycad, than in the smaller stems of the Lyginopterideae. The second point is the marked development of the anomalous medullary vascular tissues, which we have already found, as an individual peculiarity, in *Lyginopteris oldhamia*.

A small stem, from the Lower Permian of Autun, described by Renault, and named *Cycadoxylon Fremyi*, shows still more perfectly the type of structure just described. The stem is from 20 to 25 mm. in diameter; the cortex, which is fairly preserved, contains gum-canals, and large pitted elements, probably with a mechanical function. Within the cortex is a ring of normal wood and bast, both well preserved, and exactly resembling the vascular tissue of a modern Cycad. The medullary rays are extremely wide, exceeding in extent the tracheal bands between them. The tracheides are for the most part pitted; the bordered pits are ranged in numerous series on the radial walls. Towards the interior of the normal zone of wood, scalariform tracheides occur, and at its inner limit are the spiral elements of the protoxylem. It would thus appear that the whole normal wood was centrifugally developed, as is usual in recent Cycads. Professor Seward, however, states that at one place he detected a distinct strand of primary xylem; this may indicate that some trace of the mesarch structure of the Lyginopterideae

p. 386; Williamson and Scott, "Further Observations," etc. Part iii. *Phil. Trans.* vol. 186, B, 1895, p. 742; Seward, "A Contribution to our Knowledge of *Lyginodendron*," *Annals of Botany*, vol. ix. 1897, p. 65.

As Professor Seward points out, the specimen described by M. Renault in the *Flore fossile d'Autun et d'Épinac*, Part ii., under the name of *Medullosa gigas*, appears to be almost identical with Nield's plant. (But see above, p. 192.)

still persisted in *Cycadoxylon*, though much reduced. The wide phloem-zone consists of alternating concentric bands of parenchyma and sieve-tubes.

Within the normal vascular ring are two or more interrupted zones of anomalous wood and bast, with inverted orientation, the phloem facing inwards. These medullary vascular arcs are separated by parenchyma from the normal centrifugal wood. The whole structure is thus comparable to that of *Cycadoxylon robustum*, except that the normal zone is much less developed, which may simply be a matter of age.

Curiously enough, no leaf-trace bundles have so far been found in *Cycadoxylon Fremyi*. The characters, as at present known to us, strongly suggest Cycadean affinities, though the characteristic anomaly of *Cycadoxylon*, the formation of inverted zones of secondary wood and bast in the pith, is not known in the same form among recent Cycads. On the other hand, it is identical with the most frequent anatomical variation occurring in stems of *Lyginopteris oldhamia*.

Another silicified stem from the Permian of Autun, the *Ptychoxylon Levyi* of Renault, presents a somewhat similar combination of characters. In this fossil the dimensions are greater than in *Cycadoxylon Fremyi*, the stem of *Ptychoxylon* attaining a diameter of 5 or 6 cm. The external surface bears the marks of spirally disposed appendages. The character of the genus depends on the arrangement of the vascular tissues. There is an outer, more or less continuous cylinder of wood and bast, surrounding a very large pith, within which are several secondary vascular bands, with their wood developed centripetally, while that of the normal outer ring is centrifugal (Fig. 87). The traces of both leaves and branches are present, and, as the two organs appear to correspond in position, it is not improbable that the latter were axillary. It seems that the phyllotaxis was $\frac{3}{8}$.

Where the bundles of a leaf or branch pass out, the

external vascular cylinder is interrupted, and its edges are incurved, to unite with two of the internal vascular bands (see Fig. 87, x' , ph'). The latter are thus always continuous, at some point of their longitudinal course, with the normal vascular ring. This, it will be remembered,

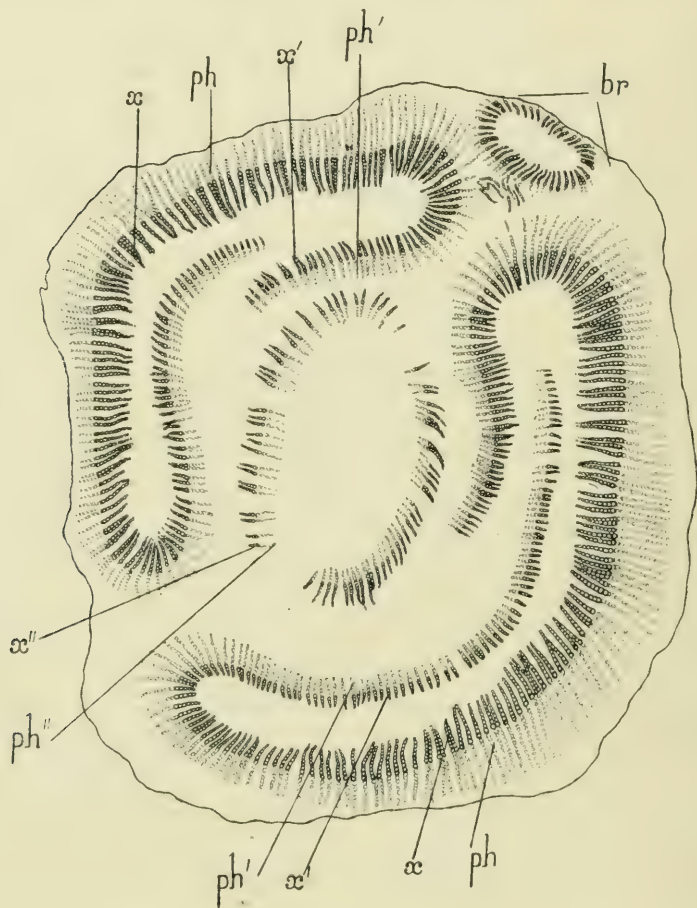


FIG. 87.—*Ptychoxylon Levyi*. Transverse section of a decorticated stem. x , ph , normal xylem and phloem; x' , ph' , first inverted medullary bands of xylem and phloem, continuous at the leaf-gaps with the normal zone; x'' , ph'' , second inverted zone; br , stele of a branch. Slightly magnified. After Renault.

is precisely what happens in some specimens of *Lyginopteris oldhamia*, where the anomalous medullary wood and bast are likewise connected, at the leaf-trace gaps, with the normal vascular tissues (see p. 40). In *Ptychoxylon*, however, the conditions are more complicated, for there are often two or three concentric systems of

internal vascular arcs, joining on at different levels to the external ring (see Fig. 87, *x''*, *ph''*).¹ The character of the wood and bast of each ring is very parenchymatous, like that of *Cycadoxylon*, or of a recent Cycad. The phloem, which is external in the case of the normal zone, but internal in each of the anomalous bands, is beautifully preserved, and even the details of the sieve-tubes have been made out. There appears to be no indication in this genus of any primary centripetal wood in the stem.

The leaf-traces, however, appear, from Renault's description and figures, to have essentially the same structure as in *Lyginopteris*: the trace consists of two bundles, side by side; in each bundle there is a large arc of secondary wood on the outer side of the primary strand; the spiral elements lie near the limit of primary and secondary wood, so it appears that the former was wholly or mainly centripetal in its development.

The parenchymatous cortex, which contains secretory sacs, or canals, is coated externally by periderm; this may account for the absence of any hypodermal fibres, which had very probably been lost by exfoliation.

The branches, at their base, had a normal vascular ring, but, as they became free, gradually assumed the complex structure of the main stem.²

The stems just described, '*Cycadoxylon robustum*, *C. Fremyi*, and *Ptychoxylon Levyi*, may be grouped under the family-name of Cycadoxyleae, a designation already used by Renault, but in a somewhat more extended sense.³ The interpretation of their structure

¹ Compare the double anomalous zone in *Cycadoxylon robustum*, Fig. 86.

² For a full description of *Cycadoxylon* and *Ptychoxylon* see Renault, "Bassin houiller et permien d'Autun et d'Épinac," *Flore fossile*, Part ii. pp. 307-21, 1896.

³ Renault included *Medullosa* and *Colpoxylon* in the Cycadoxyleae. On the view here taken, these two genera belong to a different, though related, line of descent, as has already been shown.

which, in agreement with the views of Professor Seward,¹ I desire to suggest is that they may have been derived from some form resembling *Lyginopteris oldhamia*, from which they have deviated in two principal respects. On the one hand, they have gradually lost the *primary* centripetal wood of the vascular bundles in the stem. In *Cycadoxylon robustum*, this tissue has not been recognised with certainty, and must at most have been relatively unimportant; in *C. Fremyi* it was certainly on the verge of extinction; in *Ptychoxylon* it had probably disappeared altogether. This change is in a Cycadophytic direction, for the recent Cycads (as well as the Mesozoic Bennettiteae) have wholly lost the centripetal primary wood of their vegetative stems, while retaining it in their leaves, and occasionally in the peduncles of their cones. It is very interesting to find that the leaf-trace bundles in the cortex of *Ptychoxylon* retain the *Lyginopteris* structure: in a typical Cycad they would not possess centripetal wood in this part of their course.

The extinction of the centripetal xylem was, no doubt, correlated with the advance of secondary growth. As the centrifugal wood became more and more predominant with the increasing activity of the cambium, the small centripetal portion (the "Cryptogamic" wood of the French authors) became insignificant in comparison, and could be dispensed with, so far as the stem is concerned. In the roots there was a special physiological reason, connected with the absorptive function, for its retention,² and here it has held its own all through; in the leaves, where secondary tissue-formation is less marked, it persisted in many cases, as in Cycads, Cordaiteae, and perhaps, in a modified form, in Coniferae,

¹ "Contribution to our Knowledge of *Lyginodendron*," *Annals of Botany*, vol. xi. 1897; also *Fossil Plants*, vol. iii. 1917, p. 185.

² See Strasburger, *Histologische Beiträge*, iii. p. 140; also Chauveaud, "L'Appareil conducteur des plantes vasculaires," *Ann. des Sci. Nat. Bot.*, Sér. 9, t. xiii. 1911.

but in the highly modified sporophylls, even of Cycads, it tends to disappear.¹

On the other hand, the Cycadoxyleae had changed in another direction, and one peculiar to themselves among the allied groups. The anomalous formation of inverted medullary wood and bast, which in *Lyginopteris* only appears as an individual and comparatively unimportant peculiarity, had in the Cycadoxyleae become a constant and marked character. We regard this structure as a new formation, due to the spreading inwards of cambial divisions through the leaf-trace gaps, as is clearly shown in *Lyginopteris* itself, and in *Ptychoxylon*. There is no reason to suppose that the anomalous centripetal wood thus formed had anything to do with the primary and normal centripetal wood of the more primitive forms: the example of *Lyginopteris oldhamia* shows that the two structures were quite independent. Neither does it seem practicable to derive the structure of Cycadoxyleae from a system of Medullosean steles. Scattered medullary bundles are a characteristic anatomical feature in the recent genera *Encephalartos* and *Macrozamia*,² but continuous zones or extensive arcs of inverted wood and bast do not appear to be known in the pith of normal Cycads. Such anomalies, however, as shown by similar cases in many recent Dicotyledons, are extremely variable, and the peculiarity in question cannot hinder us from recognising the generally Cycadophytic character of the stems of Cycadoxyleae.

It must always be remembered that the Cycadophyta were once an extensive and dominant class of plants, and that the few, which have survived to our own time, only give us a very imperfect and partial idea of the

¹ See Worsdell, "Vascular Structure of the Sporophylls of the Cycadaceae," *Annals of Botany*, vol. xii. 1898.

² See Worsdell, "Anatomy of the stem of *Macrozamia*," etc., *Annals of Botany*, vol. x. 1896. "The Structure and Origin of the Cycadaceae," *ibid.* vol. xx. 1906.

range of organisation which the group once exhibited. The Cycadoxyleae present, as we have seen, marked analogies with the later Cycadophytes, but it is improbable that they were on the direct line of descent (see Chap. V.).

It is interesting to find that the same Permian beds of Autun, which have yielded the stems of Cycadoxyleae, also contain both leaves and fructifications which may be of a Cycadophytic character. The leaves are referred to the genera *Pterophyllum* and *Sphenozamites*,¹ the former recalling the foliage of the recent *Dioon*, and the latter that of some species of *Zamia*. The agreement, in form and venation, with typical Cycadean leaves, is sufficiently close to render it probable that the affinities of these fossils were with the Cycadophyta.

The fructification referred to —*Cycadospadix milleryensis*, Ren.² — is a very remarkable one, represented in Fig. 88. The axis bears numerous fimbriated sporophylls (*l*), concave on their lower surface, and on the under side of each sporophyll two seeds (*s*) were borne. Renault, the discoverer, stated that the sporophylls were spirally arranged, and regarded the whole structure as con-



FIG. 88.—*Cycadospadix milleryensis*. Fructification, consisting of an axis, bearing numerous lacinate sporophylls (*l*), each of which bears seeds (*s*) (probably two to each sporophyll) on its lower surface. Slightly reduced. After Renault.

¹ See Renault, *Flore fossile d'Autun et d'Épinac*, Part ii.

² *Loc. cit.* Prof. Seward uses the generic name *Strobilites*, as the Cycad relation is doubtful.

stituting a lax cone. Some of the specimens are inserted, almost at right angles, on a branch little thicker than the axis of the cone itself. Such an arrangement is not found among true Cycads, but the comparatively slender, branched stem of the Rhaetic *Wielandiella* (see Chap. V.) offers an analogy; and as *Ptychoxylon*, at any rate, is known to have branched pretty freely, it is quite possible that Renault's interpretation is the right one. It seems not impossible, however, that the whole structure may represent a single compound leaf or sporophyll, or even a single fertile pinna, the bodies immediately bearing the seeds being of the nature of leaflets. In the latter case, we should have a sporophyll more complex than that of any recent Cycad, and its affinities would probably be with the Pteridosperms; on Renault's interpretation, the fructification would represent a nearer approach to the cones of the Zamieae. In any case the fossil is of the greatest interest, and it is much to be hoped that specimens with structure preserved may yet be discovered.

Whether these leaves and fructifications belonged to Cycadoxyleae or not, it is probable that the stems in question (or some of them) were those of plants which had already passed the boundary (at most a very indefinite one) between Pteridosperms and Gymnosperms.

SUMMARY OF THE PTERIDOSPERMS

As explained above (p. 94), we have used the name Pteridospermeae in the widest sense, to cover all the families previously included under Cycadofilices, as well as those in which there is direct evidence for the seed-habit. The reason for this extension of the denotation is the impossibility of carrying out in practice a distinction based only on the degree of strength or weakness of the evidence. The name Cycadofilices may be and has been employed in the same wide sense; the only

objection to this use of it is that it implies an affinity with Cycadophyta, which is only indicated in certain families and not throughout the whole group. Both names may be criticised on the ground that they suggest a closer relation to Ferns than appears on a reconsideration of the data to be established.

The Pteridosperms, as now understood, constituted a great and complex phylum, nearest, on the whole, to the Ferns, but independent and perhaps running as far back in geological time as any of the lines of the Vascular Cryptogams. Possibly their origin may have to be sought among plants of the Psilophytales Flora.

It is still only in very few cases that reproduction by seeds has been definitely proved among Pteridosperms—in *Lyginopteris Oldhamia*, a couple of species of *Neuropteris* and of *Aneimites*, and in *Pecopteris Pluckenetii*. There is further a considerable body of collateral evidence, varying in its degree of cogency, but sufficient to show that the seed-habit was widespread.

All the same, there are still many groups, here included under Pteridosperms, in which there is no evidence at all as to the mode of reproduction. This is the case with all the families described in Chap. II., which are characterised throughout by their vegetative structure only. Here we can judge of their systematic position solely by comparison with the anatomy of families known to include seed-bearing members, namely, the Lyginopterideae and Medulloseae, the only groups in which the structure is known which at present fulfil this condition.

The four families, Rhetinangieae, Megaloxyleae, Calamopityeae, and Stenomyeae, all have something in common with the Lyginopterideae, as shown by the well-developed primary wood, the large leaf-traces with mesarch or exarch xylem, the secondary thickening and the multiseriate bordered pits of the tracheides. The degree of affinity indicated varies greatly; the structure

is monostelic throughout, but the frequent occurrence of exarch xylem and the numerous petiolar strands in Calamopityaceae and Stenomyeleae suggest a certain approach to a Medullosean type; it will be remembered that in *Heterangium* among Lyginopterideae there is often some approximation to exarch structure, while the petioles, in several species, are polydesmic.

In any case, the four families mentioned appear clearly to belong to the same cycle of affinity with known seed-bearing groups, and there is thus a strong presumption that they too had reached the spermophytic stage.

The two families, Protopitycae and Cladoxyleae, are more isolated; their peculiarities have been sufficiently emphasised above (pp. 153, 166). We have also seen that they have certain features in common, though the general organisation of the two groups is on quite different lines. In these families we may have the relics of some very ancient stock, perhaps somewhat remote from the main body of the Pteridosperms. They certainly show no affinity to Cycadophyta, as Solms pointed out, in the case of *Protopitys*, in 1893; still, we can find no place for either family elsewhere than among Pteridosperms—a wider and greater class than the old name Cycadofilices implied. While some members of the Pteridosperm phylum no doubt led on to Cycadophyta, and others perhaps to Cordaitales, the majority in all probability led nowhere, but simply died out. The Protopitycae and Cladoxyleae were presumably among the latter.

It is unnecessary to discuss the problematic genera *Steloxylon* and *Rhexoxylon*, still imperfectly known; the former seems to have some characters in common with both Cladoxyleae and Medulloseae, but whether it really forms a link between the two diverse groups is extremely doubtful. *Rhexoxylon* no longer appears to be built on a polystelic plan, and at present stands quite by itself.

The Cycadoxyleae, as we have seen, are questionable Pteridosperms, for the almost complete loss of primary

xylem in the stem separates them from all the recognised families of the phylum. They show closer analogies with the Cycadophyta than do the Pteridosperms proper. On the other hand, *Dolerophyllum*, if the connection of the various organs described under this name were established, might probably find its place as an aberrant Pteridosperm.

It is obvious that, in the present state of our knowledge, it would still be premature to attempt to define the limits of the Pteridospermeae, or to assign them precise characters. A purely provisional diagnosis may, however, be of use for the purpose of distinguishing the class from other Palaeozoic Spermatophyta. The following characters may serve :

Plants megaphyllous.

Leaf-traces relatively large.

Primary xylem well developed, usually mesarch or exarch,
both in the stele and leaf-traces.

Secondary wood and bast formed.

Pits of the tracheides bordered, usually multiseriate.

Male and female sporophylls comparatively little differentiated from the vegetative foliage.

No cones formed.

Seeds of a Cycadophytic type, with a pollen-chamber and a highly developed vascular system.

The reproductive characters are taken from the few cases in which the fructification is known, and thus rest on a narrower basis than the anatomical part of the diagnosis. We are not yet in a position to distinguish the seeds from those of Cycadophyta or Cordaitales. The microsporangia have not been included in the provisional diagnosis, as our knowledge of these organs is still too scanty.

CHAPTER IV

THE CORDAITALES

Poroxyleae ; Pityeae ; Cordaiteae

I. POROXYLEAE

WE now pass on to a group of fossil plants, which occupies a somewhat different position from those which we have just described. We are no longer concerned with Pteridosperms, but with a class of plants more typically Gymnospermous. The group first to be considered, that of the Poroxyleae, while having much in common with certain of the Pteridosperms, especially with the Lyginopterideae and Calamopityeae, shows affinities not directly with the Cycadophyta but rather with a wholly extinct order of Gymnosperms, the important Palaeozoic family Cordaiteae. The three families, Poroxyleae, Pityeae, and Cordaiteae, are, in fact, so far interrelated that they may provisionally be grouped under the common class-name Cordaitales.

The Poroxyleae are represented at present by the one genus *Poroxylon* (of which two or three species are known). *Poroxylon* is a genus in which the available data chiefly relate to the vegetative structure ; such evidence as we possess concerning its organs of reproduction will be considered later on. Our present, very complete, knowledge of the anatomical structure, which is preserved in astonishing perfection, is due to the

investigations of the two French palaeobotanists, Renault and the elder Bertrand.¹

The genus was originally discovered in the Permo-Carboniferous deposits of Grand Croix and Autun, in France. The two best-known French forms, *Poroxylon Boysssetii* (which includes the specimens first discovered, and described by Renault in 1879) and *P. Edwardsii*, only differ from each other in unimportant characters, which may or may not be of specific value.

The stems of these plants were comparatively slender, the specimens described not much exceeding half an inch in diameter; they bore spirally arranged leaves, separated from each other, for the most part, by rather long internodes; the French authors worked out the phyllotaxis from the course of the leaf-trace bundles, and found the divergence between two successive leaves to be $\frac{5}{13}$. The leaves themselves were very different in character from those of any of the Pteridosperms, as at present known. They were broad, thick, simple leaves, inserted on the stem by a definite petiole, and tapering towards the opposite extremity. The lamina was traversed by numerous parallel veins.² This is quite a different type of leaf from anything we have met with among the groups already considered.

The structure of the stem, however, is of a type already familiar to us. The transverse section of a young stem is represented in Fig. 89, B. We see at once that there is a well-marked pith, surrounded by a ring of collateral vascular bundles. The primary xylem-strands of these bundles, which border immediately on

¹ B. Renault, *Tiges de la flore carbonifère*, 1879; C. E. Bertrand et B. Renault, "Les *Poroxylons*," in *Archives bot. du Nord de la France*, 1886.

² The leaves, or at least their laminae, do not appear to have been found in connection with the stem, in these species; but, as Bertrand and Renault pointed out, the close anatomical agreement between stem and leaf established a strong presumption that the two organs belonged to identical or closely related species.

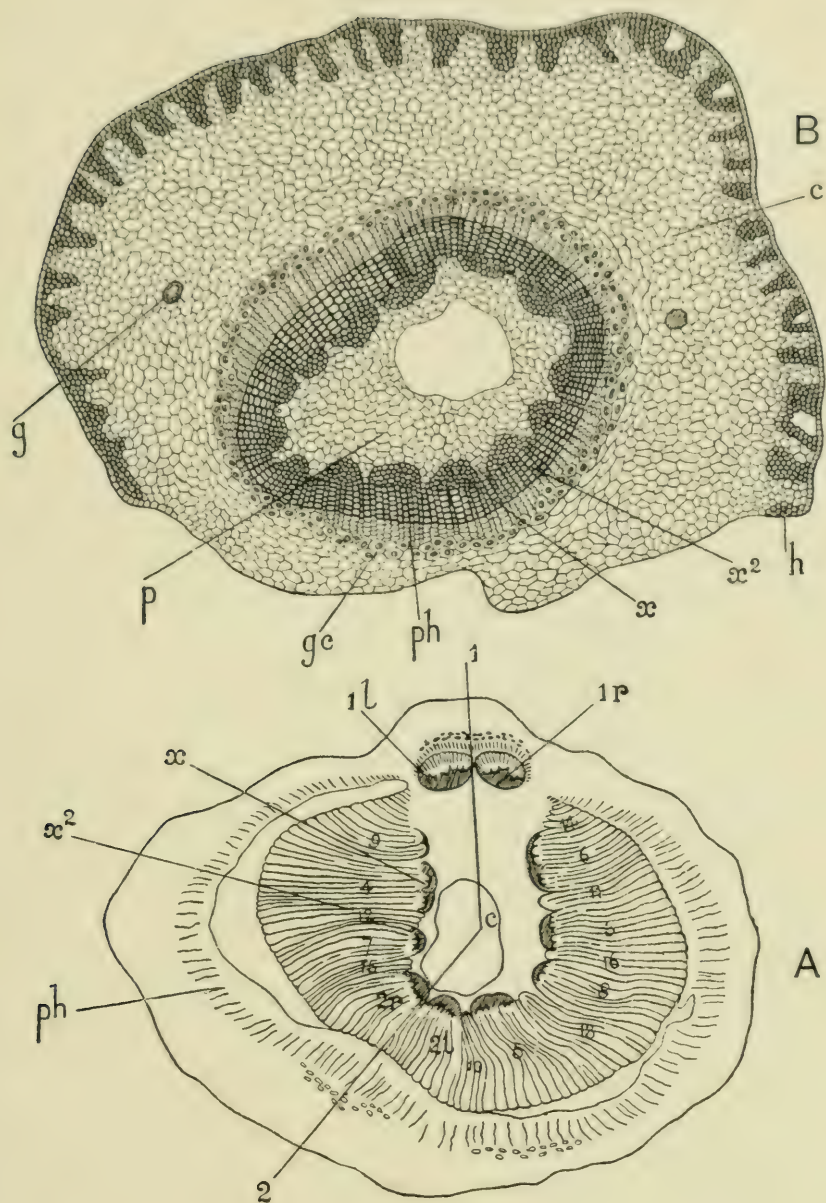


FIG. 89.—A, *Poroxyton Edwardsii*. Transverse section of stem. *c*, cavity in pith; *x*, primary wood of bundles, which are numbered in the order of the $\frac{1}{3}$ phyllotaxis, No. 1 belonging to the lowest leaf of the series; the angle 1, *c*, 2, is that of the divergence between two successive leaves; 1*l* and 1*r*, the two bundles constituting the outgoing leaf-trace; *x*², secondary wood; *ph*, phloem. \times about 5. After Bertrand and Renault. B, *P. Boysssetii*. Transverse section of young stem. *p*, pith; *x*, primary wood of bundles; *x*², secondary wood; *ph*, phloem; *gc*, secretory (?) sacs or canals; *g*, mucilage-canal; *c*, cortex; *h*, hypoderma. \times 7. After Renault.

the pith, are clearly marked off from the surrounding zone of radially arranged secondary wood, which is succeeded externally by the well-preserved cambium and phloem. The stem thus had secondary growth in thickness, of a normal character. The pericycle, immediately surrounding the phloem, and the inner primary cortex, contain structures interpreted as gum-canals, and similar organs are also present in the pith. The outer cortex was strengthened by a system of hypodermal strands of sclerenchyma, such as we have so often met with in the stems of Palaeozoic plants. The general anatomy of the stem is thus strikingly similar to that of a *Lyginopteris*, and a more detailed examination shows that the resemblance is a real one. A general agreement with *Calamopitys* is also evident.

The bundles surrounding the pith are rather more numerous than in *Lyginopteris*, a fact which is correlated with the more complex phyllotaxis of *Poroxylon*. Each leaf-trace, on entering the stem from a leaf, runs down through thirteen internodes before joining the trace of a leaf vertically below. Hence, in any transverse section of the stem, the traces of thirteen successive leaves are met with (see A, Fig. 89).

The internodes are long, and, as the leaf-trace traverses the cortex in about half the length of an internode, it follows that in any transverse section of the stem not more than one outgoing trace (if any) is shown (see Fig. 89, A and B). Each leaf-trace, in the upper part of its course, consists of a double bundle. It will be remembered that in *Lyginopteris* also the leaf-trace is a double one. In that genus, however, the two strands of the trace unite, as we follow them inwards through the pericycle (see Fig. 11, p. 23); in *Calamopitys* they unite in the same region (Fig. 54, p. 119), or in the zone of thickening, whereas in *Poroxylon* they remain distinct for some distance below their entry into the interior of the stele. Thus, the two strands of primary wood

shown in Fig. 90 both belong to the same leaf-trace, which (proceeding from the second leaf above) has already taken up its position at the margin of the pith.

This figure also serves to illustrate the important point that the development of the primary xylem of the bundles was *centripetal*. At the level of the section each of the twin-bundles has two protoxylem-groups (*px*), separated by parenchyma from the secondary wood on

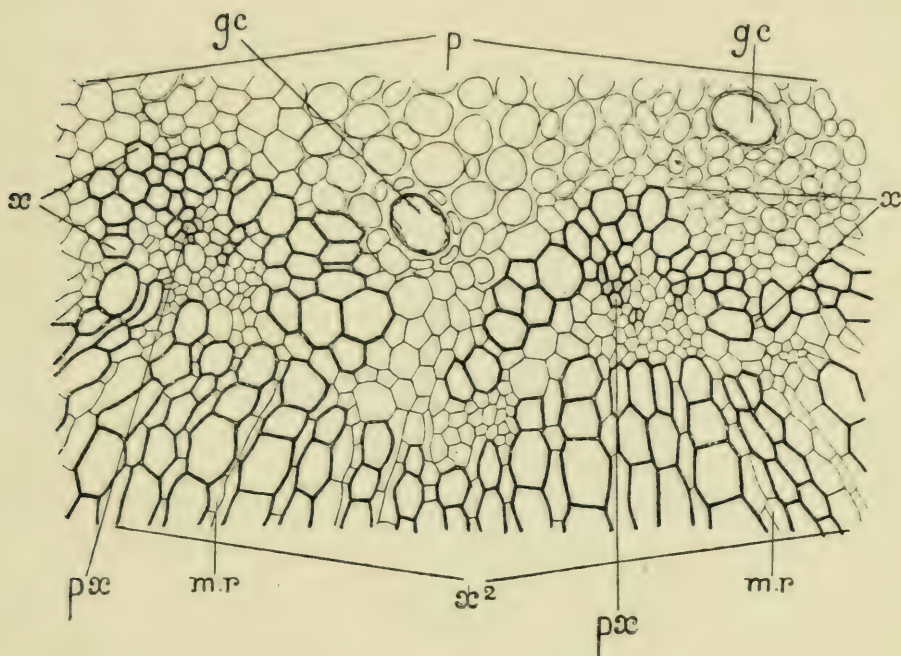


FIG. 90.—*Poroxylon Edwardsii*. Transverse section of the stem, showing two primary xylem-strands, with adjacent tissues. *p*, pith; *gc*, mucilage-canals; *px*, protoxylem; *x*, primary centripetal xylem; *x*², secondary xylem; *m.r.*, medullary rays. $\times 66$. After Bertrand and Renault.

their exterior side. The centripetal xylem of each strand forms an arc, abutting, at its ends, on the secondary wood. The whole structure is strikingly like that in *Lyginopteris* (cf. Fig. 13, p. 26), except that, so far as has been observed, there is no centrifugal primary xylem in the case of *Poroxylon*.

The elements adjoining the spiral protoxylem are scalariform, while the more internal parts of the centripetal wood consists of pitted elements; we may compare

Lyginopteris or *Heterangium* (p. 91). Traced further downwards in the stem, the structure of the primary wood becomes simplified; the protoxylem-groups fuse with each other, and ultimately die out. It is a fact well known to anatomists that the spiral elements often disappear in the lower part of the course of a bundle, as is very clearly seen in the Fern *Osmunda*, the structure of which is in some respects comparable to that of the plants under consideration. Eight internodes below the node the centripetal xylem also disappears, leaving only the wedge of secondary wood to mark the position of the trace (see Fig. 89, A, bundles 10-14; cf. *Calamopitys Beinertiana*, p. 127). The communication between the different leaf-traces was kept up by lateral fusions during their passage down the stem.

The secondary wood presents no peculiarities; it consists of regular, radial series of tracheides, with medullary rays between them. The rays are of considerable height, and two or three cells in thickness; the tracheides have several rows of round or hexagonal bordered pits on their radial walls. The structure, in fact, is identical with that of the wood in *Lyginopteris*, so that the two could scarcely be distinguished. There is also a close resemblance to the wood of *Eu-calamopitys*.

The secondary phloem, which is extraordinarily well preserved, is traversed by the medullary rays, and made up of alternate tangential bands of sieve-tubes and parenchyma. *Poroxylon* is one of the few fossil plants in which the structure of the sieve-tubes can be made out. A radial section of *P. Edwardsii* is figured by Bertrand and Renault, in which the numerous compound sieve-plates on the radial walls are perfectly plain, just as in some recent Cycads. *Heterangium tiliacoides*, *Medullosa anglica*, and *Stauropteris oldhamia*, among British fossil plants, sometimes rival *Poroxylon* in the perfection with which the phloem is preserved.

The French authors state that there is no pericycle,

distinct from the primary phloem. That is a matter of interpretation, but it is an interesting point that the formation of periderm took place on the inner border of the cortex, and immediately outside the "primary phloem"—in fact, in just the same position which it occupied in *Lyginopteris*. In the older stems, the whole of the cortex was thrown off as bark, a stage which has not been observed in the latter genus, though *Calamophytis* may offer analogies.

The double leaf-trace, as it passes out through the cortex, preserves its collateral structure, and is accom-

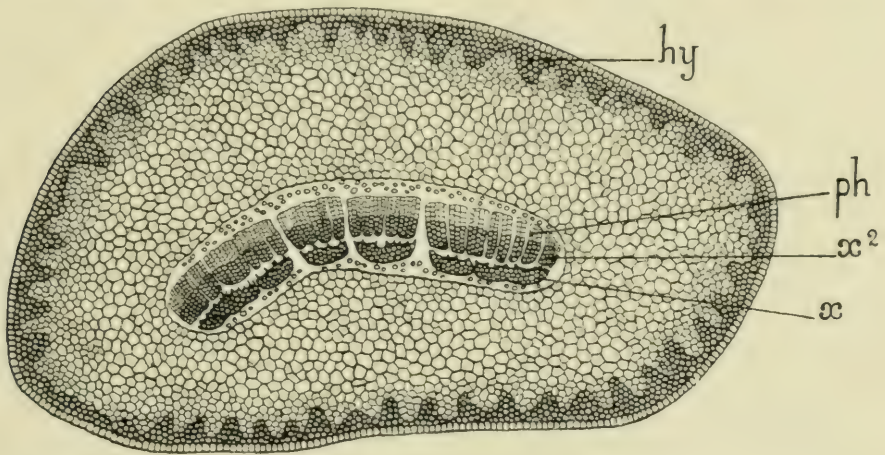


FIG. 91.—*Poroxylon Boyssettii*. Transverse section of petiole. x , primary xylem; x^2 , secondary xylem; ph , phloem; hy , hypoderma. \times about 10. After Renault.

panied by secondary wood and bast on its outer side. The same structure is maintained in the leaf itself. Fig. 91 represents a transverse section of the petiole of *P. Boyssettii*. The vascular bundles, which have begun to subdivide, are arranged in a transverse series, the phloem facing downwards and the xylem upwards, as is usual in leaves; they present essentially the mesarch structure of the bundles of Cycadean leaves (cf. Fig. 15, p. 27) with all the centrifugal xylem secondary. The petiole, like the stem, had a strong mechanical construction, owing to the presence of hypodermal ribs of sclerenchyma (Fig. 91, hy).

The petiole widened out gradually into the broad simple lamina, which was traversed by numerous parallel bundles, derived from the subdivision of those of the petiole, and branching dichotomously. The larger bundles, which are crowded together in the median region of the lamina, have the same structure as those in the petiole; the finer strands, toward the edges of the leaf, are simplified, and no longer show any centrifugal wood. Just the same simplification of structure occurs in the smaller bundles of the leaf, in recent Cycads. The lamina was of considerable thickness, and was stiffened by the usual hypodermal fibrous strands on both surfaces. The dense mesophyll is said to show some traces of palisade-like arrangement. The larger bundles of the lamina were connected by transverse bridges of thick-walled elements.

Grand'Eury¹ subsequently identified the leaves of *Poroxylon* in the form of carbonaceous impressions. He finds that they are of great size, reaching a length of a metre, with a breadth of .15 to .20 metre. They are narrowed at the base, passing insensibly into the petiole.

In these leaves we have a highly remarkable organisation, totally different from anything met with, either in the Ferns or among the genera associated under the Pteridospermeae. The detailed structure is, in fact, that of a Cycad, but the leaf of *Poroxylon* was a simple not a compound one, so that the whole leaf has been compared to a single leaflet of a Cycad such as *Bowenia*.

In the fact that the vascular bundles retain collateral structure throughout the leaf, *Poroxylon* agrees with *Medullosa* but differs strikingly from *Lyginopteris*, in which, as described above (pp. 33 and 45), the structure becomes concentric as the petiole is entered. We shall see presently that the leaves of *Poroxylon* present the closest analogies with those of the Cordaiteae.

¹ " Sur les *Rhabdocarpus*, les graines et l'évolution des Cordaïtées,' *Comptes rendus*, t. cxi. p. 995, 1905.

An interesting point in the morphology of the genus *Poroxylon* is the fact that the stem bore axillary branches, thus presenting a further analogy with some forms of *Lyginopteris*. The vascular system of the branch was inserted on the two bundles of the main axis, between which the trace of the subtending leaf passed out. Thus, in the section shown in Fig. 89, A, the branch, if present, would have been in vascular connection with the bundles marked 6 and 9. The first few internodes of the branch were short, and the first leaves probably rudimentary, judging from the small development of the leaf-traces supplying them. In its upper part, the branch assumed the same structure as the main stem.

Poroxylon appears to have possessed a complex branch-system, for shoots are found of very different calibre, independently of differences due to age.

Roots and rootlets, which have been found in association with *Poroxylon Boyssetii* and *Edwardsii*, agree so exactly, in the structure of their histological elements, with the stems of those plants as to leave no reasonable doubt that Bertrand and Renault were justified in referring them to the genus *Poroxylon*. The rootlets, in particular, are perfectly preserved, and their anatomy has been fully investigated. The structure is, as a rule, diarch; in a few cases a tetrarch cylinder has been observed. The anatomy of the roots and rootlets is, in all respects, such as characterises Gymnospermous roots at the present day. In the usual case of diarch organisation, the secondary wood and bast form two large masses, one on either side of the primary xylem-plate, while a broad ray corresponds to each of the two protoxylem-groups at the ends of the plate. In the details of wood and phloem the roots agree precisely with the stem. The whole cortex was thrown off at an early stage by the formation of pericyclic periderm. Thus the outer surface of the root was formed by a layer of cork, just as in the roots of *Medullosa anglica*,

described in the last chapter, or in those of recent Gymnosperms.

Bertrand and Renault were able to observe the mode of insertion of the rootlets on the main root, and to determine that the plane of the diarch xylem-plate coincided in the two organs. This is a point of interest, for, as is well known from the researches of Prof. van Tieghem and others, this arrangement is characteristic of the roots of Gymnosperms and Phanerogams generally, while, in the case of the diarch roots of Vascular Cryptogams, the plane of the xylem-plate of the rootlet lies at right angles to that of the parent root. It will be recalled that *Lyginopteris* agrees with *Poroxylon* in this respect also.

Our summary has been based on the discoveries of Bertrand and Renault; the anatomy was worked out in the most elaborate detail by the French investigators, owing to whose labours this genus became one of the most completely known, so far as the vegetative organs are concerned, among fossil plants.

An English species, described in the second edition of this book under the name *Poroxylon Sutcliffi*, has now been made the type of the new genus *Mesoxylon*, an account of which will be found under Cordaiteae.

We have still no certain information as to the fructification of *Poroxylon*. On grounds of association, however, Grand'Eury¹ attributed the seeds known as *Rhabdocarpus*, Brongniart, to these plants, with which he also found "floral axes, bearing large and long male and female buds, without bracts." *Rhabdocarpus*, as limited by Brongniart, is a genus of seeds with bilateral symmetry, characterised by the presence of numerous fibrous strands in the sarcotesta. The seeds are of the same general type as those of the Cordaiteae, described below (see p. 305). Fig. 92 shows a seed of this genus in transverse section, displaying the characters of the platy-

¹ See his paper above cited, "Sur les *Rhabdocarpus*," etc.

spermic type. The discovery, if confirmed, will considerably strengthen the affinity otherwise indicated between the Poroxyleae and Cordaiteae.

Bertrand and Renault regarded the genus as related, on the one hand, to *Sigillaria*, and, on the other, to Cordaiteae. The affinity with the Cordaiteae seems indisputable, as will appear when we come to describe that family; the relation to *Sigillaria*, however, though it appeared tenable at the time it was suggested, and was supported by the case of *Sigillariopsis*, with its double

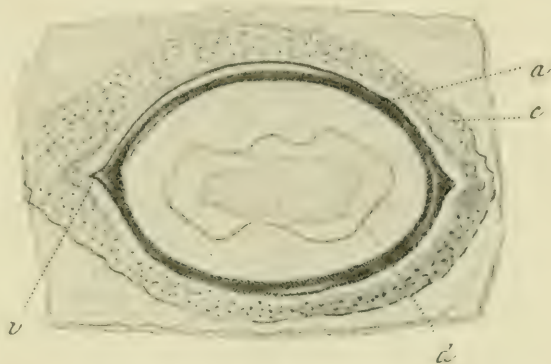


FIG. 92. — *Rhabdocarpus subulnicatus*, Grand'Eury. Transverse section of seed, to show the platyspermic type of structure. *a*, sclerotesta; opposite the ridge (*v*) at each side is a vascular bundle; *c*, sarcotesta, with numerous fibrous strands; *d*, contracted nucellus, within which is the embryo-sac. \times about 3. After Brongniart.

foliar bundle and occasionally pitted tracheides (see Vol. I. p. 207), now seems to be excluded by the manifest affinity between *Poroxylon* and the Pteridosperms of the *Lyginopteris* group. As has been already pointed out, and as the French observers recognised, the agreement in structure between *Poroxylon* and *Lyginopteris* is in many respects a close one, so much so that there can scarcely be a doubt that the two genera are allied. The same remark applies, to a great extent, to the Calamopityeae also. The Pteridosperms, however, as is now abundantly proved, were a distinct stock, showing certain analogies with the Ferns, and the inference appears justified that *Poroxylon* also, though more modified, was derived from this independent phylum and not from a Lycopodinean stock. The importance of this conclusion will become evident when the Cordaiteae have been considered.

II. THE PITYEAEE

Before going on to the Cordaiteae we will shortly consider a group of fossil plants which evidently constitute a separate family, though they may be provisionally regarded as forming part of the wider group which we call Cordaitales. Our knowledge of the group has considerably increased of late years.

Most of the stems in question fall under the genus *Pitys* of Witham,¹ as emended by Göppert.² There are now four species of *Pitys*, all from the Lower Carboniferous of Southern Scotland ; three of these were described by Witham in his famous pioneer work of 1833. The species are chiefly distinguished by the width of the medullary rays, the principal rays being as much as seven cells wide in *P. primaeva*, five or six cells in *P. antiqua*, and four cells in *P. Withamii*. *Pitys Withamii* is the well-known Craigleith tree, of which a trunk is set up in the grounds of the Natural History Department of the British Museum. A stem of this species found at Craigleith, near Edinburgh, in 1830, was 47 feet in length ; at the top, the wood still had a diameter of 1½ foot. The fourth species, *P. Dayi*, Gordon, will be described below.

The pith and wood are the only parts preserved in Witham's species, as at present known. Our knowledge of *P. Dayi* is more complete. The wood, except for the greater width of the principal medullary rays, is of the Araucarian type, and so far, as we shall see, agrees with that of the Cordaiteae (cf. Fig. 101, p. 274) ; the secondary tracheides have multiserial bordered pits, confined for the most part to their radial walls.

¹ *The Internal Structure of Fossil Vegetables found in the Carboniferous and Oolitic Deposits of Great Britain, described and illustrated*, Edinburgh, 1833, p. 71.

² "Revision meiner Arbeiten über die Stämme der fossilen Coniferen," *Botan. Centralblatt*, Bände v. and vi. 1881.

A point of great interest is the presence, in all these species, of a number of small strands of primary wood, disposed around the pith.¹ This structure is well shown in *Pitys antiqua*, the Lennel Braes tree, from which the illustration in Fig. 93 is taken. The imperfectly discoid pith is large, sometimes as much as 2 inches across; in a specimen where the pith measured only 22 mm. in diameter, the number of xylem-strands round the pith was between forty and fifty. The diameter of each xylem-strand is small, averaging about .25 mm.; most of the strands are embedded in the pith at some little distance from the inner edge of the woody zone (Fig. 93), with which they only come into contact when about to make their exit as leaf-traces. Where a xylem-strand passes out into the zone of secondary wood, its place is taken by a reparatory strand lying behind it, deep in the pith. The outgoing strand shows some sign of division into two, but the two halves appear to reunite further out in its course. Branching and anastomosis of the strands are found at many places.

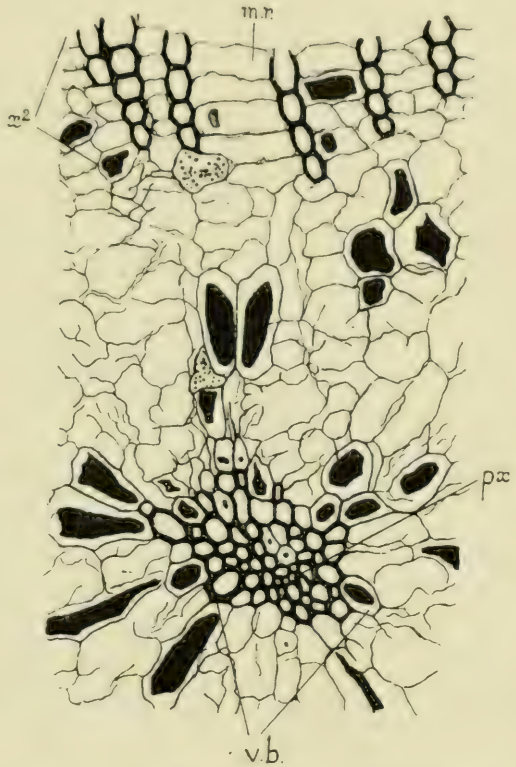


FIG. 93.—*Pitys antiqua*. From a transverse section of the stem. *v.b.*, primary xylem-strand embedded in the pith; *p.x.*, protoxylem; *x²*, inner part of secondary wood; *m.r.*, medullary rays. The cells with black contents may be secretory sacs. $\times 73$. Kidston Coll. 598A. (G. T. G.)

¹ Scott, "Primary Structure of certain Palaeozoic Stems," etc., *Trans. Roy. Soc. Edinburgh*, vol. xl. part ii. 1902.

In the great majority of the xylem-strands the structure is definitely mesarch, the spiral protoxylem-elements lying in the interior (Fig. 93, *px*). The primary tracheides are accompanied by a little xylem-parenchyma.

No spiral elements could be detected at the inner edge of the woody zone, so it would appear that the primary wood is represented only by the medullary strands. The considerable separation between the latter and the main zone of wood is difficult to account for, and suggests some specialisation of function, as, for example, that the primary strands might have become superfluous for the main work of water-conduction and have served to supply the bulky parenchymatous pith.

The mesarch xylem-strands, in spite of their reduced size and the peculiarities of their arrangement, are evidently comparable to those of the Lyginopterideae and Calamopityeae. On the other hand, the arboreal habit has suggested an affinity with the Cordaiteae.

In the specimens originally observed, the primary xylem-strands were found, as already described, to be limited to the peripheral part of the pith. That they were not necessarily restricted to this region has been shown by the researches of Prof. W. T. Gordon, whose work has in various points greatly extended our knowledge of the anatomy and morphology of the genus. Prof. Gordon has kindly permitted me to insert an account, in his own words, of his unpublished observations, illustrated by photographs which he has supplied, reproduced in Figs. 94-96. By way of preface to his remarks it is necessary to mention that a new genus, named *Archaeopitys*, Scott and Jeffrey, chiefly distinguished by the presence of xylem-strands throughout the whole of the pith, had already been described, from the Lower Carboniferous of Kentucky. We shall return to this genus later. Prof. Gordon's statement is as follows :

" The discovery of several small twigs of a new type

of *Pitys* (*P. Dayi*) in Lower Carboniferous rocks at Gullane, East Lothian, has thrown more light on the structural features of this genus and has rendered its correlation with the Cordaitales less probable than has been supposed.

“The specimens vary from 1·5 to 2 inches in diameter, and in many cases are still clothed in bark (Fig. 94),

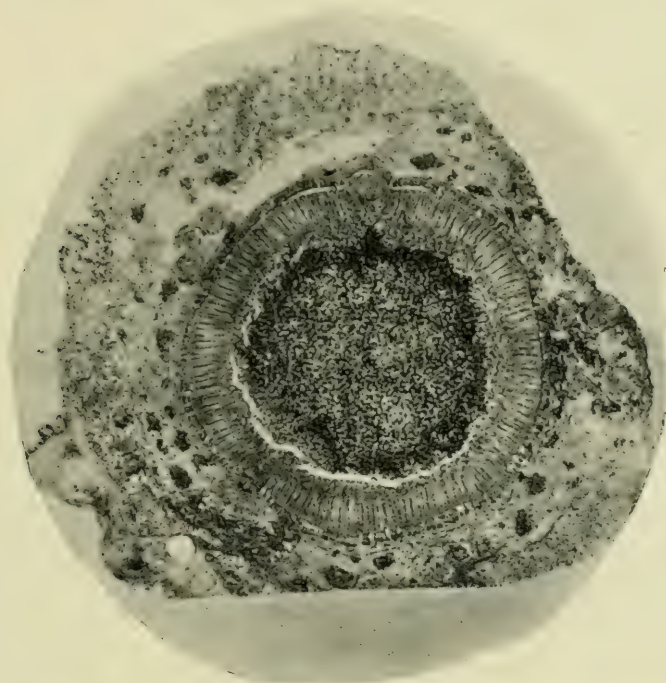


FIG. 94.—*Pitys Dayi*. General transverse section of stem, showing pith, wood, and cortex. Leaf-traces are seen, both in the wood and cortex; the latter are dividing up into concentric strands. $\times 3$. From a photograph by Prof. W. T. Gordon.

while two examples terminated in buds with leaf-bases and petioles still attached.

“In no case has any indication of the reproductive members been discovered and therefore the affinities must be based on purely vegetative characters.

“The axis in all the specimens consists of a wide, parenchymatous non-discoidal pith surrounded by a ring of xylem (Fig. 94). The primary strands are, as usual in *Pitys*, separated from the secondary wood by a zone of parenchyma, two or three cells deep. But there

are other strands more deeply immersed in the pith, a circumstance recalling the structure of *Archaeopitys Eastmanii*, Scott and Jeffrey. These additional strands are scattered through the whole pith, but are generally



FIG. 95.—*Pitylites Dayi*. Transverse section of stem, showing pith, with part of secondary wood and cortex. In the pith the medullary and circum-medullary xylem-strands can be made out. A leaf-trace is passing out through the wood. $\times 10$. From a photograph by Prof. W. T. Gordon.

smaller than the circum-medullary types (Fig. 95). So far it has not been possible to follow the course of these inner strands throughout their length.

“The circum-medullary bundles, on the other hand,

have been traced out into the petioles. On its passage outwards the bundle increases in size and then divides into three, though exceptionally five bundles have been noted (Figs. 94, 95). In every case actually traced into a petiole there were only three strands, and these persisted throughout the length of the leaf. It is interesting



FIG. 96.—*Pitys Dayi*. Transverse section of leaf, showing the sclerenchymatous cortex, the ground-tissue, and the three vascular bundles. $\times 18$. From a photograph by Prof. W. T. Gordon.

to note that in *Araucaria excelsa* the bundle supplying the leaf divides into three, though only the median of these persists throughout the length of the leaf.

“The free petiole is a short fleshy member with a marked hypoderma and three bundles clearly distinguishable in transverse section (Fig. 96). The length exceeds

1.5 inches and the whole tapers gradually to a sharp point. No sign of a lamina occurs, and from the general appearance of the end of the petiole it is practically certain that no lamina ever existed. To compensate for this the petiole has enlarged into a stout fleshy organ.

"All these vegetative characters are strikingly similar to corresponding characters in *Araucaria*, especially *A. excelsa*. The wide pith, the intimate characters of the tracheides, the leaf-trace bundle with three branches, the short fleshy petioles and absence of lamina are characters common to both *Pitya* and *Araucaria*. The spatulate or Poa-like leaf of *Cordaitea* is quite distinct from this *Pitya* type.

"Where branches have been observed passing out from any of these new stems a group of the circum-medullary bundles runs out from the main axis, but the details of branch emission have not yet been ascertained.

"The new features exhibited by *P. Dayi* were so interesting that the older species were re-examined, and specimens of *P. antiqua* and *P. primaeva* have also been found to possess immersed bundles in addition to the circum-medullary strands. Yet the sections, examined by Dr. Scott in 1899, did not show these immersed bundles, and the exact conditions under which such strands may develop have not so far been determined. Further search among the new specimens may throw some light on this point.

"The new evidence then correlates *Pitya* more closely with *Archaeopitya* and at the same time widens the gap between these genera and the members of the Cordaitan alliance. It also indicates Araucarian affinities, particularly with these forms which possess uninerved leaves like *A. excelsa*. Boyd Thomson's case for the great antiquity of the Araucarian alliance seems to get considerable support from these new specimens."¹

¹ A brief summary of Prof. Gordon's results was given in Seward's *Fossil Plants*, vol. iii. 1917, p. 288.

The great importance of Prof. Gordon's observations is manifest. His new species, *P. Dayi*, is at present the only member of the Pityeae in which the cortex and leaves are known, and thus throws more light on the position of the family than all the rest. Before entering on any further discussion, however, it is desirable to describe other forms referred to this group.

A new genus, *Archaeopitys*, was founded in 1914, on a species, *A. Eastmanii*, one of the fossils from the base of the Waverley Shale (Lower Carboniferous) of Kentucky.¹ At the time the original description was written only one specimen was available; the maximum diameter of the incomplete fragment was 2.7 cm., and that of the pith about 5.5 mm. Since then I have received a second specimen from Prof. Jeffrey, forming part of a larger stem, about 4.5 cm. in diameter as preserved, with a large pith about 3 cm. diameter. Neither specimen includes anything outside the secondary wood; the second one, however, shows the exit of the leaf-traces, which the former did not. Hence it has now been possible to determine with certainty the upper and lower ends of the specimen.²

The xylem-strands in the pith are the chief feature; about half of these strands lie at the margin of the pith, while the rest are scattered all through its substance. The former may be called circum-medullary, the latter simply medullary strands. The structure of each xylem-strand is mesarch, as in *Pitys*, and the dimensions of the strands not very different from those of that genus. Where a leaf-trace passes out, one of the circum-medullary strands divides into two; the inner branch becomes a reparatory strand and remains in the pith, while the

¹ D. H. Scott and E. C. Jeffrey, "On Fossil Plants, showing Structure, from the base of the Waverley Shale of Kentucky," *Phil. Trans. R. Soc. Series B*, vol. 205, 1914, p. 345.

² It turns out that this was done wrongly in the case of the original specimen; we have, therefore, to reverse the words "downward" and "upward" in the description given in the Kentucky memoir.

outer makes its exit through the wood, and constitutes the leaf-trace, which is thus a single bundle at its origin. It is interesting to find that, as the trace approaches the outer border of the wood, it becomes completely surrounded by its own secondary zone of xylem, like the leaf-traces of *Pitys Dayi*, figured by Prof. Gordon (Fig. 94). Some signs of division of the trace have been observed, but could not be followed far enough for comparison with the divisions in *P. Dayi*.

The secondary wood is dense, compared with that of the *Pitys* species. The density is due, partly to the small size of the tracheides, partly to the relatively small number of the wider medullary rays, which may attain a thickness of five or six cells. The rays are all rather short and most of them comparatively narrow. The pitting is badly preserved, but two or three rows of pits on the radial tracheide-wall could be made out in places.

In the light of Prof. Gordon's results it seems doubtful whether the genus *Archaeopitys* can be kept up, for the main character on which it was founded (the presence of xylem-strands throughout the whole pith) proves to be common to various species of *Pitys*, though not always constant. It is better, however, to maintain the genus provisionally, until the publication of Prof. Gordon's researches in full allows of a more exact comparison with *Pitys*.

Another genus allied to *Pitys* is *Callixylon*, founded by Dr. Zalesky¹ on a species, *C. Trifilievi*, discovered by him in the Upper Devonian of the Donetz Basin in South Russia. The plant is thus of special interest from its age. The preservation of the specimens is excellent, but does not extend beyond the wood.

Callixylon differs from *Pitys* and *Archaeopitys* in the

¹ Zalesky, "Communication prélim. sur un nouveau *Dadoxylon* à faisceaux de bois primaire," etc., *Bull. de l'Acad. Imp. des Sciences de St-Petersbourg*, 1909, p. 1175; "Étude sur l'anatomie du *Dadoxylon Tchihatcheffi*," *Mém. Comité Géol.* livr. 68, 1911, p. 28.

fact that all the primary xylem-strands are circum-medullary, and usually in contact with the secondary wood, though occasionally a few cells may intervene (Fig. 97). The strands are mesarch, and in all respects similar to those of *Pitya antiqua*, the resemblance extending to the radial elongation of the adjacent medullary cells and to the detailed structure of the pith as a whole.

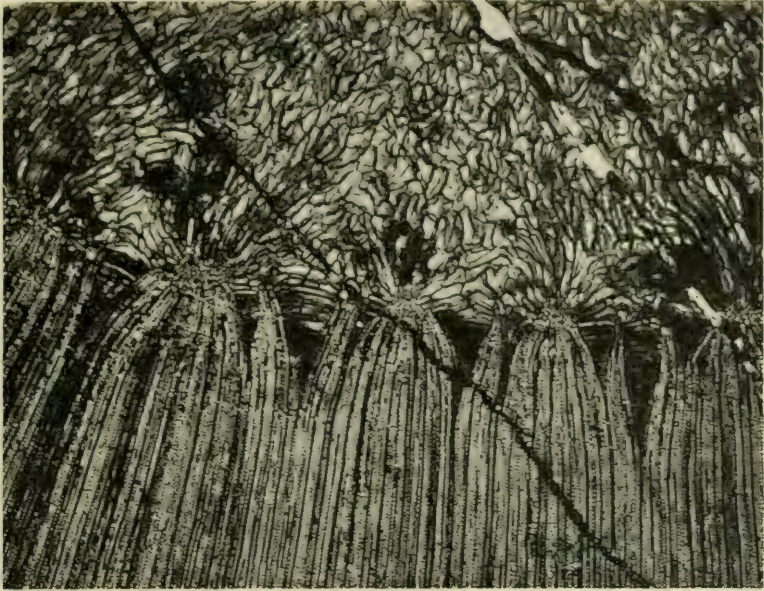


FIG. 97.—*Callixylon Trifilievi*. Part of transverse section of stem, showing part of the pith, and five primary mesarch xylem-strands, corresponding to the wedges of secondary wood. One of the strands is double. \times about 14. From a photograph supplied by Dr. Zalessky.

The exit of the leaf-traces has not been described ; Prof. Seward¹ suggests that the occurrence of twin-bundles (as shown at one place in Fig. 97) may indicate that the trace was double. This, of course, is not conclusive ; a somewhat similar approximation of two bundles has been observed in *Archaeopitys*, where the leaf-trace was single.

The structure of the secondary wood presents some points of interest. It is divided, towards the pith, into wedges, each wedge corresponding to one of the circum-medullary strands (Fig. 97). The inner ends of the

¹ *Fossil Plants*, vol. iii. p. 291.

medullary rays, between the wood-wedges, are much dilated, but elsewhere the rays are narrow, usually only one cell in width ; this is a striking difference from *Pitys*, and even from *Archaeopitys*, in which wide rays also occur. The pitting is of the usual multiseriate, bordered type, but the distribution of the pits is remarkable. They are not uniformly distributed on the radial walls, but form definite pitted areas, separated by tracts of unpitted cell-wall. The pitted areas of consecutive tracheides are ranged in regular radial series, giving a very characteristic appearance to the radial sections. Tangential pits occur, as in *Pitys antiqua*.

Two American species, *Callixylon Newberryi* and *C. Oweni*, of Upper Devonian age, have been placed in this genus, on account of the well-marked characters of the secondary wood ; the primary structure of these species has not yet been observed.¹

The genus *Callixylon* is of great interest, as the oldest known representative of the family. That it really belongs to the Pityeae seems to be proved by the agreement of the primary structure (pith and xylem-strands) with that of *Pitys*, if we choose for comparison specimens (such as those originally described in *P. antiqua*) in which the xylem-bundles are limited to the peripheral zone of the pith. At the same time there are definite distinctions both in the position of the primary strands and in the secondary wood-structure, which fully justify generic separation.

Dr. Zalesky also compared the structure of his plant with that of *Parapitys* (formerly *Dadoxylon*) *Spenceri*, a fossil which was described under the heading Pityeae in the second edition of these "Studies." A relationship is by no means out of the question, but it now seems more natural to consider *Parapitys* in connection with the Cordaiteae (see p. 282).

¹ Elkins and Wieland, "Cordaitean Wood from the Indiana Black Shale," *American Journal of Science*, vol. xxxviii. 1914.

The discovery of the leaves of *Pitys* by Prof. Gordon puts the affinities of the group in quite a new light. Such leaves have nothing in common with those of the Cordaiteae (see p. 289), and seem rather to suggest an approach to the "needles" of a Conifer. Prof. Gordon's comparison of his plants with certain Araucarias is of great interest, and when further developed will, no doubt, have an important bearing on the affinities of the Coniferae. In the meantime it is already evident that the Pityeae form a more independent family than was realised before, as shown both by their anatomical and morphological characters. We continue to include them under the wide class Cordaitales on grounds of convenience, but we can no longer say, as was said in the second edition of this book, that they lead up to the family Cordaiteae. It is a somewhat striking fact that the most highly differentiated wood-structure in the Pityeae is found in the oldest genus, the Devonian *Callixylon*. This suggests a high antiquity for the family.

III. THE CORDAITEAE

We now pass on to a family which belongs beyond question to the true Gymnosperms. The Poroxyleae and Pityeae are at present chiefly or solely known to us by their vegetative characters; we have now to deal with a group in which our evidence is drawn from all the organs of the plant—reproductive as well as vegetative. Though even here our knowledge is but limited and urgently needs to be extended, the fact remains that the family in question—that of the Cordaiteae—is one of the best known, as it is also among the most remarkable, of those which fossil botany has revealed to us.

Among the vegetable remains from the Carboniferous strata, specimens were long ago observed, such, for example, as fragments of petrified wood, which presented

Coniferous characters, while others, such as the impressions of large parallel-veined leaves, suggested at first sight Monocotyledons of the *Yucca* type. Associated with these remains, fossil catkin-like inflorescences (*Antholithus*) were sometimes found, as well as a considerable variety of seeds, of the bilateral type. The piecing together, on sure evidence, of these remains, apparently so diverse, and the revelation of their structure, was essentially the work of the two French investigators, Grand'Eury and Renault,¹ though valuable contributions from other hands have not been wanting.

1. *External Characters.*—We may begin by stating the general results of the reconstruction which has been arrived at, and then go on to describe the organisation of the various organs more in detail. The Cordaiteae were tall, somewhat slender trees, with trunks rising to a great height before branching, and bearing at the top a dense crown, composed of branches of various orders, on which simple leaves of large size were produced in great abundance (Fig. 98). The stumps of the trees, with the roots attached, have often been found; the root system is said to have been rather feebly developed. The stems, in their present state, attain a diameter of a couple of feet or more, which is small in comparison with the height of the trees, for Grand'Eury found that in various specimens the shaft alone (below the crown) reached a height of 10, 20, or even 30 metres. It must be remembered, however, that the large specimens have their wood reduced to coal, so that the total diameter was no doubt considerably greater in the natural state than appears from the fossil remains.

The leaves were borne in a spiral sequence, on the ultimate branches; they were simple elongated leaves,

¹ See especially Grand'Eury, *Flore carbonifère du Département de la Loire*, 1877, and Renault, *Structure comparée de quelques tiges de la flore carbonifère*, 1879.

varying considerably in form in different members of the group; on these differences genera or sub-genera



FIG. 98.—*Dorycordaites*, sp. Restoration, showing roots, trunk, and crown, the latter composed of branches bearing large lanceolate leaves and inflorescences. The trunk is shown too short. After Grand'Eury. Modified.

have been founded. Thus, in the typical *Cordaites* (*Eucordaites*) the leaves are spatulate, with blunt ends;

they reached in some cases a length of a metre, and a width of 15 cm. To this group the forms most fully investigated belong (see Fig. 99). Then we have *Dorycordaites*, with leaves little inferior in length to those of the last group, but lanceolate and sharply pointed. Our Fig. 98 represents a restoration of a tree belonging to this sub-genus. Finally there is *Poacordaites*, with grass-like leaves, reaching half a metre in length, by only a centimetre or so in breadth. The leaves of Cordaiteae, whatever their form may have been, are all characterised by parallel venation, giving them much the appearance of Monocotyledonous leaves, such as those of a *Yucca* or *Dracaena*; consequently, the earlier writers on fossil botany always placed these fossils in the class Monocotyledons. The veins are repeatedly forked, except in the narrow leaves referred to *Poacordaites*. In many instances branches have been found, bearing the leaves (cf. Fig. 99), or marked by the scars due to their fall. The scars are usually transversely elongated, and sometimes bear the prints of the vascular bundles which entered the leaf. The leaves were crowded in some forms, more remote in others, but there was always a free internodal surface between their insertions. In some cases a lateral twig is found in an early stage, as a large leaf-bud, as shown in Fig. 99.

The habit of the Cordaiteae must have been different from that of any trees with which we are now familiar. The species with comparatively short leaves may be compared with such Coniferae as *Agathis* (e.g. the Kauri Pine of New Zealand), or with certain forms of *Podocarpus*, and these trees may best serve to give us some idea of the appearance of the extinct family. But the longer-leaved species must have had a habit very different from anything which we are accustomed to associate with Gymnosperms at the present day.

Branches showing the characteristic marks of *Cordaites* were found by Grand'Eury with structure pre-

served, and this important discovery enabled palaeobotanists to identify a large proportion of the apparently



FIG. 99.—*Cordaites laevis*. Branch (restored) bearing the large spatulate leaves, with parallel venation, and the inflorescences, each with numerous catkins. A large bud is also shown. Reduced. After Grand'Eury.

Coniferous woods of the Palaeozoic strata, named *Araucarioxylon* or *Dadoxylon*, as belonging to the Cordaiteae.

The anatomical structure will be described below ; here it is only necessary to say that the large size of the pith, sometimes attaining a diameter of nearly 4 inches, is characteristic of these plants, and at once distinguishes their stems from those of the Coniferae.

Casts of the pith-cavity of *Cordaitea*s are well-known and characteristic fossils, which used to be called *Artisia* or *Sternbergia*. They are cylindrical, or somewhat ribbed casts, sometimes very slender, but usually an inch or more, and sometimes approaching 4 inches, in diameter, and marked by numerous transverse constrictions at very short intervals, so that the whole resembles a pile of coins. Williamson, in 1851,¹ found a cast of this kind still enclosed in wood, which proved on investigation to have the structure of *Araucarioxylon*. This was one of the first steps made towards the reconstruction of these fossils, for we now know that the wood in question, resembling that of the recent *Araucarias*, belonged to certain members of the Cordaiteae. The peculiar appearance of the casts, as Williamson explained, is due to the discoid structure of the pith, such as is found, not only in the Walnut, and in some *Jasmineae* and *Euphorbiaceae*, but also in certain species of *Pinus*, at the present day. The pith undergoes transverse rupture in many places, so as to leave numerous diaphragms separated by empty spaces. The constrictions on the cast in the fossil specimens mark the position of the diaphragms (cf. Fig. 101, A).

The recognition of the true nature of *Sternbergia* has proved important, for by this means the large, rooted stumps, found in the Coal-measures of the Loire, containing *Sternbergia* casts, have been identified as belonging to Cordaiteae.

The fructifications of the Cordaiteae were known, so far as their external characters are concerned, long before

¹ "On the Structure and Affinities of the Plants hitherto known as *Sternbergiae*," *Mem. Manchester Lit. and Phil. Soc.* ser. ii. vol. ix. 1851.

their nature was recognised. These fossils, which were at first placed in the provisional genus *Antholithus*, consist of a simple or branched stalk, bearing laterally little catkin-like bodies, not often exceeding a centimetre or so in length. The male and female catkins cannot always be distinguished externally; in some forms, however, the axis of the female inflorescence appears to have borne solitary ovules, accompanied only by a few bracts.

Grand'Eury was so fortunate as to find inflorescences such as these in connection with the leaf-bearing shoots of *Cordaite*s. An example (more or less restored) is shown in Fig. 99, where we see a leafy branch bearing several fertile peduncles, each of which in its turn bears a number of catkins, probably female. The inflorescences appear to have been inserted a little above the subtending leaves, and not immediately in their axils.

We see, then, that the connection of all the organs—stems, roots, leaves, and catkins—has now been established, at least for some species of the genus *Cordaite*s. The other genera or sub-genera are at present less completely known. We will now go on to consider the internal organisation of the various parts, beginning with that of the stem.

2. *The Stem, Cordaite*s.—The general type of structure of the stem of *Cordaite*s was that of a Conifer, but the pith, as we have seen, was far larger than we ever find it in the Coniferae, and in its dimensions rather resembled that of a Cycad. It has already been mentioned that, in many cases (though probably not in all), the pith was discoid, as shown in Fig. 101, A. This structure was no doubt due to the fact that the more central part of the pith was not able to follow the growth of the stem in length, and consequently split across at short intervals, leaving gaps between the persistent diaphragms. At the outer edge, next the wood, the medullary tissue remained continuous.

In those specimens which were originally referred to

Cordaiteae, the wood, unlike that of the Poroxyleae and Pityeae, was wholly centrifugal in its development, the first-formed spiral elements lying on the interior margin, next the pith (Fig. 101, B, *px*); they are localised in groups, often projecting somewhat into the pith, and marking the position of the primary bundles. In the genus *Mesoxylon*, however, to be described below, centripetal xylem was present.

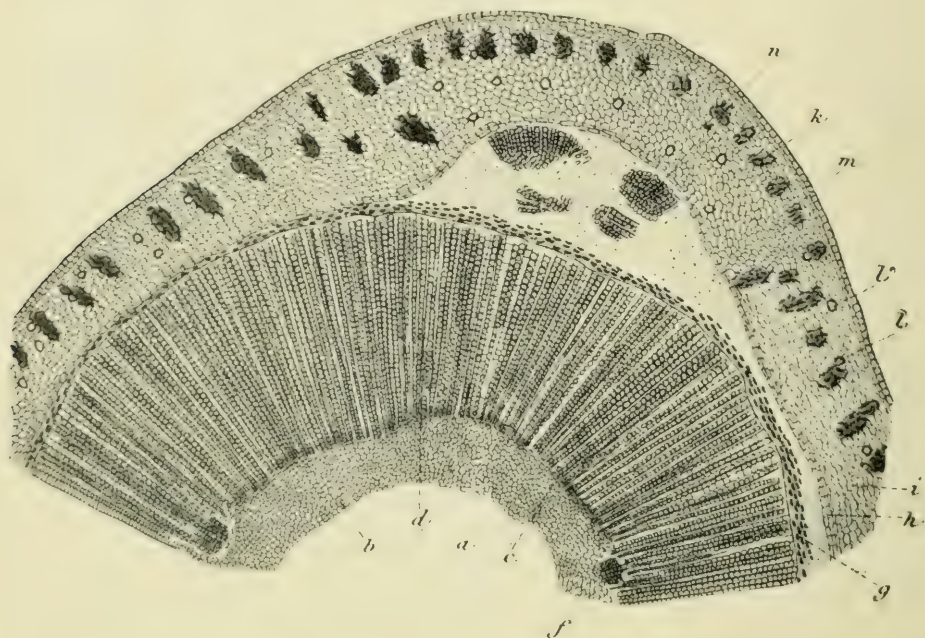


FIG. 100.—*Cordailes*, sp. Part of transverse section of a young branch, showing outer pith, wood, bast, and cortex. *a*, empty space between two diaphragms; *b*, outer, persistent zone of pith; *c*, inner zone of wood (cf. Fig. 101, B); *d*, outer zone of wood; *f*, vascular strand about to pass out; *g*, probable phloem; *h*, commencement of periderm; *i*, cortex, containing gum-canals, *l*, and fibrous strands, *k*; *n*, outgoing leaf-trace, dividing; *m*, epidermis. $\times 10$. After Renault.

In Cordaiteae of the type described by Renault, the elements of the wood are radially arranged throughout, so that in transverse sections there is no marked distinction between primary and secondary xylem (see Fig. 100). In radial sections, however, such as that from which Fig. 101, B, was drawn, we find a regular progression, from the pith outwards, in the structure of the walls of the tracheides. The narrow spiral elements of the proto-

xylem are succeeded by wider spiral tracheides, and these again by scalariform elements. It is not until many rows have been passed that we come to the pitted tracheides (*bt*) which form the bulk of the wood. The transitional region between primary and secondary xylem was thus more extensive in these plants than in most of the recent Conifers.

The secondary wood has essentially the structure of that of *Araucaria*, and was hence named *Araucarioxylon* by Kraus,¹ a name which is now superfluous in cases where the connection with *Cordaite*s has been established. The bordered pits, which are limited to the radial walls, are usually in two or more rows, and are densely crowded in alternating series, the borders thus having a hexagonal outline (Fig. 101, B, *bt*). In good material, the pore of the pit can be recognised clearly, and has the form of an inclined elliptical slit. Certain variations in the diameter of the tracheides of successive zones were regarded by Renault as indicating periods of growth, but, generally speaking, annual rings cannot be distinguished.

The medullary rays are narrow ; the principal rays, between the original bundles, may be as much as three cells in thickness, but the secondary rays are usually one, or at most two cells thick. The narrow rays have been used to distinguish the wood of *Cordaite*s from that of other families, such as *Poroxyloae* and *Calamopityeae*, but the distinction does not always hold good.

We see, then, that, so far as the secondary wood is concerned, the structure of *Cordaite*s is indistinguishable from that of a Conifer, of the family *Araucarieae*.

The phloem, when preserved, shows a radial arrangement of its elements, corresponding to that in the wood.

¹ The names *Dadoxylon*, of Endlicher, and *Araucarites*, of Göppert, are often used in the same sense as *Araucarioxylon*. *Dadoxylon* is preferable in so far as it does not suggest any affinity with the *Araucarieae*.

Sieve-tubes and phloem-parenchyma have been distinguished, and in some forms bast-fibres are also present.

The parenchyma of the primary cortex was traversed by secretory sacs, and strengthened by many radial bands

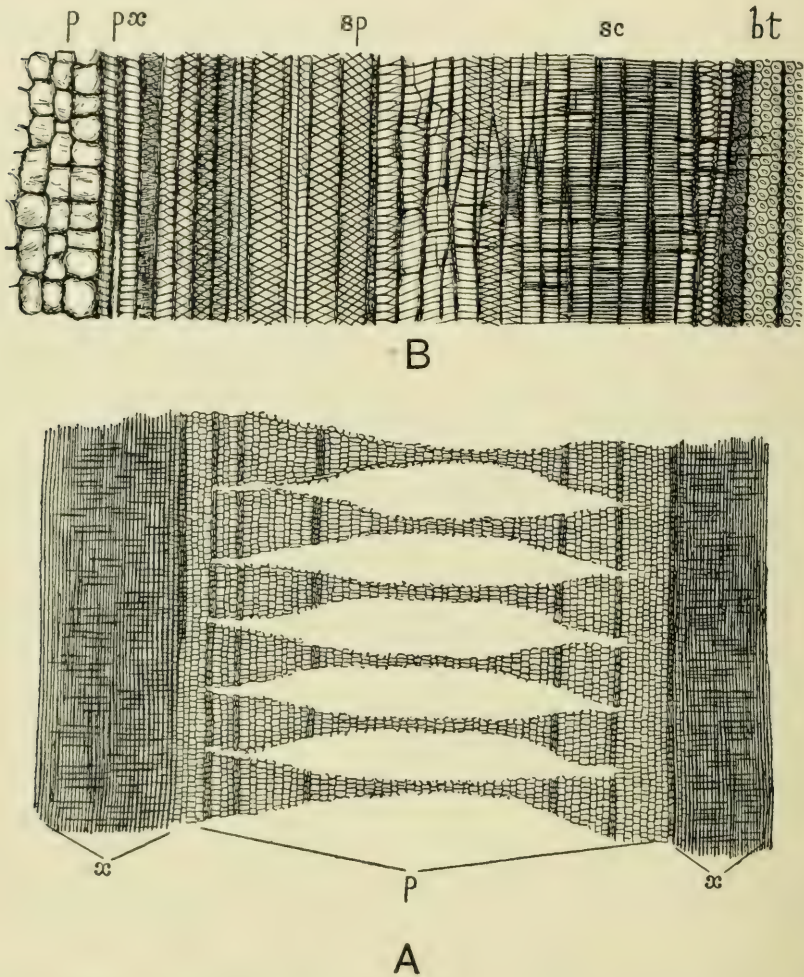


FIG. 101.—*Cordaites (Araucarioxylon) Brandlingii*. A, Radial section (somewhat restored) of middle part of stem, showing discoid pith (*p*) and wood (*x*). \times about 7. B, Inner part of wood, with adjacent cells of pith, in radial section. *p*, pith-cells; *px*, narrow spiral tracheides of protoxylem; *sp*, wider spiral tracheides; *sc*, scalariform tracheides; *bt*, tracheides with bordered pits. \times 95. Kidston Coll. 185 (Coal-measures of Dudley). (G. T. G.)

of fibres, which formed a hypodermal system, and also extended deeply into the inner cortical tissues (Fig. 100, *k*). These fibrous strands have a vertical course, and are rarely found to anastomose.

The bundles passing through the cortex on their way to the leaves are often met with in transverse sections of the stem (Fig. 100, *n*). The leaf-trace was very often a double one, a point to which Williamson called attention long ago, as offering a close analogy with *Ginkgo* among recent Gymnosperms.¹ It will be remembered that we have found a double leaf-trace in *Lyginopteris*, *Ptychoxylon*, *Poroxylon*, and other cases. The character, from its frequency in Pteridosperms and the early Gymnosperms, appears to have considerable taxonomic significance—a suggestion borne out by modern work on the occurrence of the double leaf-trace in recent Gymnosperms, and in Angiospermous seedlings.²

The large stems of *Cordaite*s are known to have formed a thick and complicated bark, but its development has not yet been satisfactorily worked out.

Mesoxylon.—Renault stated in 1896 that the stem of *Cordaite*s is “absolutely deprived of centripetal wood,” the leaf-traces only acquiring it on entering the leaf. The genus *Mesoxylon* was founded in 1910 for stems of a Cordaitean character in which centripetal xylem is present in the stele, where it forms part of the leaf-traces at the margin of the pith, and throughout their outward course. The genus is thus intermediate between *Cordaite*s and *Poroxylon*, resembling the latter in the important character referred to, but agreeing so closely in anatomical details with the former that it finds its natural place in the family Cordaiteae.³

¹ Williamson, “Organisation of Fossil Plants of Coal-measures,” Part xii. p. 470, *Phil. Trans.* 1883, Part ii. The trace became subdivided; in some forms of *Cordaite*s it has been observed that a number of bundles entered the base of the leaf.

² Ethel N. Thomas, “A Theory of the Double Leaf-trace, founded on Seedling Structure,” *New Phytologist*, vol. vi. 1907, p. 77.

³ D. H. Scott and A. J. Maslen, “On *Mesoxylon*, a New Genus of Cordaitales: Preliminary Note,” *Ann. of Bot.* vol. xxiv. 1910, p. 236; A. J. Maslen, “The Structure of *Mesoxylon Sutcliffii*,” *ibid.* vol. xxv. 1911, p. 381; D. H. Scott, “The Structure of *Mesoxylon Lomaxii* and *M. poroxylodes*,” *ibid.* vol. xxvi. 1912, p. 1011; “The Structure

Five British species of *Mesoxylon* are known at present, all recorded from the Lower Coal-measures of Shore, Littleborough, though they certainly occur at other localities. In fact, it is probable that the majority of stems and leaves from the Lower Coal-measures, loosely referred to *Cordaites*, really belonged to *Mesoxylon*. In some respects the new genus has come to be better known than its long-established fellow.

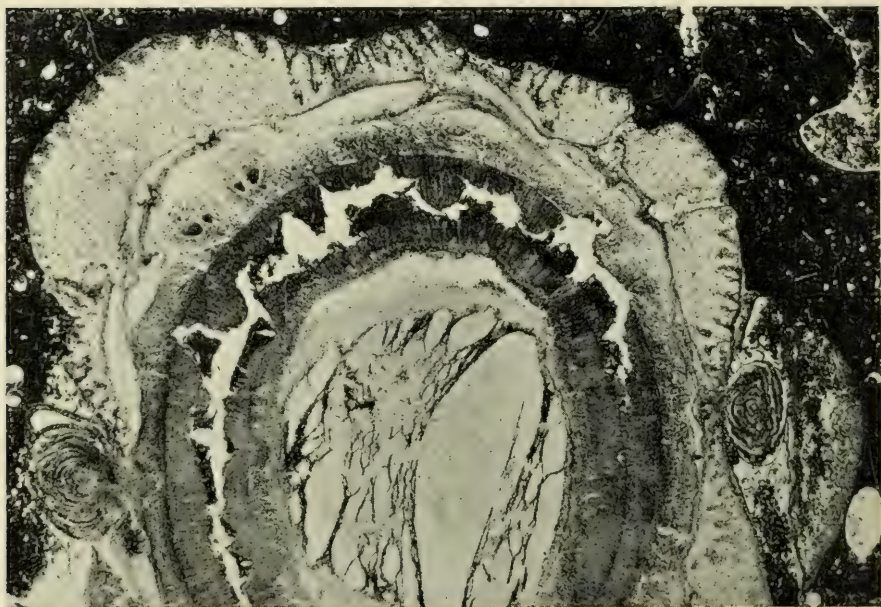


FIG. 102.—*Mesoxylon Sutcliffii*. Transverse section of stem, showing the large pith, the ring of wood and phloem, and the cortex, with leaf-bases attached, into which the leaf-traces are entering. Two axillary buds are shown; the one to the right is accompanied by the subtending leaf-base. \times nearly 4. From a photograph by Mr. L. A. Boodle. S. Coll. 2617.

One species, *M. Sutcliffii*, was figured and shortly described in the second edition of this book, under the name *Poroxylon Sutcliffii*; it has since been fully investigated by Mr. Maslen (Fig. 102). Throughout the genus, the leaf-trace is double (see diagram, Fig. 103); the centripetal xylem forms an arc on the inner side of each strand,

of *Mesoxylon multirame*," *ibid.* vol. xxxii. 1918, p. 437; "On the Fertile Shoots of *Mesoxylon* and an Allied Genus," *ibid.* vol. xxxiii. 1919, p. 1.

and the protoxylem is accompanied by a few parenchymatous cells. The centrifugal portion is continuous with the secondary wood (Fig. 104). The illustration, from *M. poroxyloides*, shows a xylem-strand, after the two bundles of the trace have already fused at the margin

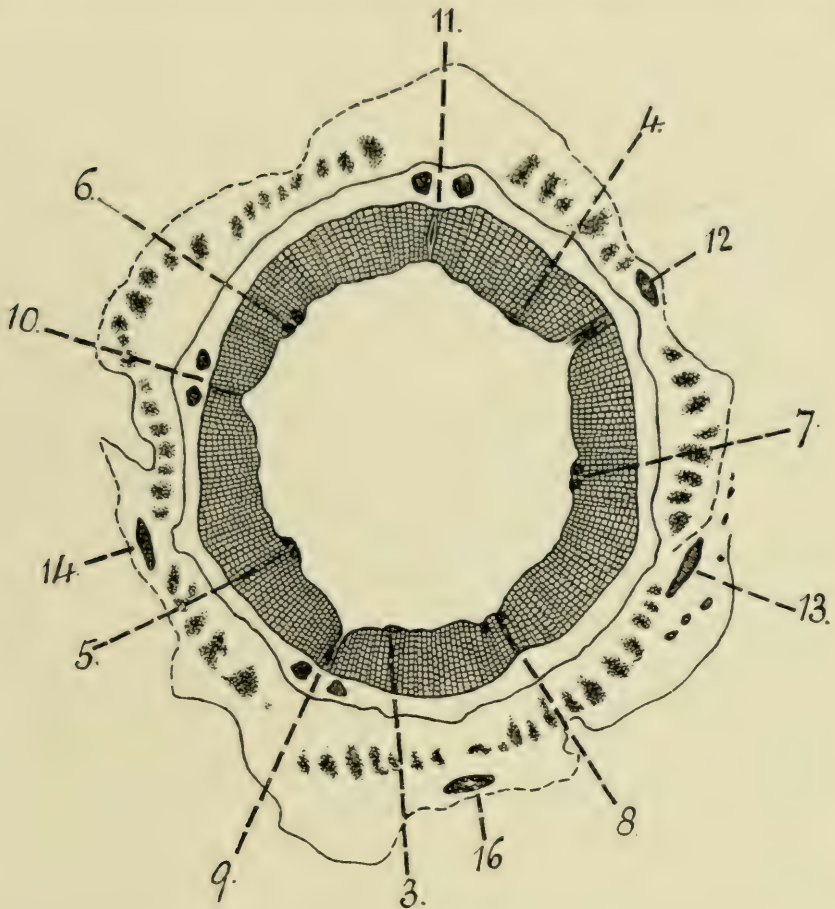


FIG. 103.—*Mesoxylon multirame*. Somewhat diagrammatic transverse section of stem. 3-16, leaf-traces, or their axillary steles (in 12, 13, 14 and 16), numbered from within outwards. Traces 1 and 2 had already disappeared at this level, and trace 15 was lost. \times about 3. S. Coll. 2334. (G. T. G.)

of the pith. The centripetal xylem is very distinct, though not so extensively developed as it would be higher up in the course of the trace. The protoxylem, as in the foliar bundles of the Cordaiteae and of Cycads, is in contact with the centripetal wood. The latter usually consists of spiral tracheides, closely wound,

except in the protoxylem itself. The centrifugal xylem, corresponding to the leaf-trace strands, consists of spiral, scalariform, and transitional elements, continuing for some distance before the typical pitted structure of the secondary wood is assumed. In all these respects there is a close agreement with *Cordaïtes*, except for the presence of centripetal xylem. In the intermediate wood, lying between the leaf-traces, a region of scalariform elements may be present or practically absent, according to the species.

There is a difference in the structure of the leaf-strand from *Poroxylon*, in which pitted tracheides occur in the centripetal xylem as well as throughout the centrifugal portion.

A general section of *M. Sutcliffii*, a species in which the stem is densely clothed with leaf-bases, is shown in Fig. 102. The double leaf-traces, in passing out through the cortex, subdivide, eight bundles entering the leaf-base. In the petiole of *M. Sutcliffii*, Mr. Maslen found as many as sixteen. Followed downwards into the stem, the behaviour of the leaf-traces varies in the different species. In *M. Lomaxii* and *M. poroxyloides* the twin-bundles converge as they reach the pith and almost immediately fuse, retaining their centripetal xylem for some distance below the fusion (Fig. 104). In *M. Sutcliffii* and *M. multirame*, on the other hand, the two strands of the trace remain distinct at the edge of the pith for a long distance before being merged; they retain their centripetal xylem about as far as they remain independent. But, in all cases, this tissue dies out gradually downwards, as in *Poroxylon*, *Calamopitys Beinertiana*, and other cases. In *M. platypodium* the twin-strands are very far apart in the pith, and begin to subdivide before the wood is passed. This species is peculiar, in so far as the leaf-trace bundles in the cortex form two distinct rows of four each. All eight enter the very broad leaf-base, from which the name of the species was taken.

Axillary shoots have been found in three out of five species, namely, in *M. Sutcliffii*, *M. multirame*, and *M. platypodium*. In *M. Sutcliffii*, where a shoot appears to be present in the axil of every leaf, they take the form of little leafy buds (Fig. 102). Their leaves are of the nature of scales and presumably the buds were resting. In *M. multirame* the axillary shoots, though more localised,

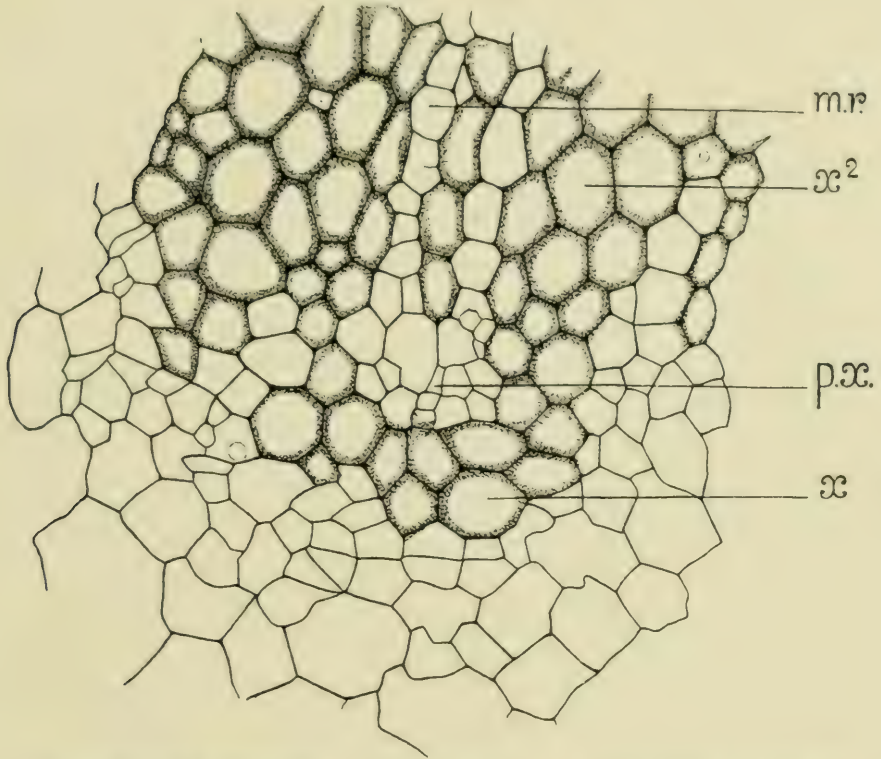


FIG. 104.—*Mesoxylon poroxyloides*. Transverse section of a xylem-strand at the edge of the pith, below the union of the two strands of the leaf-trace. *x*, centripetal xylem; *px*, protoxylem; *x*², secondary wood; *m.r.*, medullary ray. \times about 200. S. Coll. 2354. After a drawing by Miss G. C. Harrison.

are almost equally common, but quite different in structure; each is a perfectly leafless axis, with a stele much flattened in the tangential plane. As we shall see presently, these naked shoots were doubtless the stalks of the inflorescences.

In *M. platypodium*, only the steles of the axillary branches have been observed. Two or more steles occur

in the axil of the leaf, subtended by the eight bundles of the double trace. In *M. Sutcliffii* and *M. multirame* the axillary stele, traced inwards, sometimes divides in the cortex or in the wood, but the steles of *M. platypodium* are so far apart that it seems as if they must have belonged to separate buds in the same axil.

As regards the structure of the secondary wood of *Mesoxylon*, there is a close agreement with that of *Cordaites*. The medullary rays are uniseriate, or may be locally biseriate. Two features have been observed in the wood of *M. multirame*, which are rare in Palaeozoic stems: one is the occurrence at some places of tangential pits on the tracheides, a character otherwise recorded only in *Pitys antiqua* and *Callixylon Trifilievi* among Palaeozoic Gymnosperms. The other is the presence of xylem-parenchyma, forming vertical strands in the wood; this, too, had been previously noticed in *Pitys antiqua*.

The phloem is very well preserved in some specimens, especially those of *M. multirame* and *M. Sutcliffii*. It is made up of approximately tangential bands of larger and smaller elements. The larger appear to represent resiniferous tubes; the smaller are of two kinds, phloem-parenchyma and sieve-tubes; in favourable cases the sieve-plates on the inclined walls of the latter have been recognised. The pericycle contains large sacs, perhaps of a secretory character.

In most stems of *Mesoxylon* there is a zone of internal periderm, usually starting on the outer edge of the pericycle, but sometimes, as successive layers appeared, cutting deeply into the underlying tissue. In the large stems referred to *M. Lomaxii* the periderm or secondary cortex reaches a great thickness, while in *M. platypodium*, where the specimens are young, it had scarcely begun to appear. In *M. Sutcliffii*, Mr. Maslen found a well-marked abscission-layer at the base of the leaf—a rare feature in Palaeozoic plants.

The outer cortex is generally of the *Dictyoxylon* type,

with a network of hypodermal fibrous bands. In *M. platypodium* the bands of fibres run vertically with occasional connections.

In four out of the five species, the pith is known to have been discoid, as in *Cordaitea*; while the outer zone is persistent and continuous, the middle region has been broken up into diaphragms with empty spaces between them. In *M. platypodium* alone, the structure of the pith could not be determined, owing to the state of preservation.

The genus *Mesoxylon*, while agreeing closely in anatomical structure with *Cordaitea*, provides an interesting link between this group and the Poroxyleae, on account of the presence of centripetal xylem in the stem. The fertile shoots, which afford further evidence of the *Cordaitea* connection, will be considered below.

It may be mentioned that two of the species, *M. Lomaxii* and *M. platypodium*, occur in roof-nodules, while the other three are found in the ordinary coal-balls formed in the seam.

Dr. Zalesky kindly informs me that he has discovered a new species of *Mesoxylon*, *M. Demetrianum*, Zal., in coal-balls from the Coal-measures of the Donetz Basin in South Russia. As he points out, his species, while quite distinct from any of ours, has most in common, as regards the course of the primary xylem-strands, with *M. Lomaxii* and *M. poroxyloides*.

Mesoxyloopsis.—Another genus, named *Mesoxyloopsis*, with the one species, *M. Arberae*, has been founded for stems from the same source as *Mesoxylon*, but differing in the smaller size of the pith and more especially in the fact that the leaf-trace departs from the stele as a single and not a double bundle. In other respects the specimens agree with the previous genus.¹

Buds of *Mesoxyloopsis* are known, with the young leaves attached; these leaves are broad and have many

¹ See Scott, 1919, above cited.

bundles ; they are clearly of the Cordaitean type. The single leaf-trace divided repeatedly in traversing the cortex to supply the vascular system of the leaf.

Parapitys.—A stem described in the second edition of "Studies," under the name *Dadoxylon Spenceri*, has since been placed in the new genus *Parapitys* by Dr. Zalesky.¹ The structure of the plant indicates a place among the Cordaiteae rather than the Pityeae, as was previously suggested. *Parapitys Spenceri* is a fossil found near Halifax ; there has been some doubt as to its horizon, which was probably low down in the Upper Carboniferous.

The stem has a small, obtusely pentagonal pith, apparently not discoid, and a very dense secondary wood with the tracheides narrow and the medullary rays almost always uniseriate. The leaf-traces are given off from the angles of the pith in pairs ; the comparison with *Ginkgo* in this respect was already suggested by Williamson, who first described the fossil. At the edge of the pith and in contact with the woody zone, there are pairs of small, primary xylem-strands, corresponding to the leaf-traces. Traced downwards the strands of each pair fuse ; they are distinctly mesarch in the upper part of their course, but at a lower level the centripetal xylem appears to die out, as in *Mesoxylon* and other cases. The mesarch structure is characteristic, for in *Parapitys* the centrifugal part of the strand is evidently primary, whereas in *Mesoxylon* it is merged in the secondary wood.

The interest of *Parapitys* thus lies in its combining the wood-structure of the Cordaiteae with primary xylem-strands like those of *Lyginopteris* or *Calamopitys* in a reduced form.

¹ D. H. Scott, "Primary Structure of certain Palaeozoic Stems," etc., *Trans. Royal Soc. Edinburgh*, vol. xl. Part ii. 1902, p. 357 ; M. Zalesky, "Étude sur l'anatomie du *Dadoxylon Tchihatcheffi*," *Mém. Com. Géol., St Pétersbourg*, N.S., livr. 68, 1911, p. 28.

Caenoxylon.—This is one of Dr. Zalesky's new genera, and is founded on a stem of Upper Palaeozoic age (*C. Scotti*, Zalesky), perhaps from the Permian of the Ural. There is a large pith, 2 cm. in diameter, and surrounding it are a number of strands of primary xylem, much broken up, the pith intruding between them. All these strands, though sharply marked off from the secondary wood, are *endarch* in structure, no centripetal xylem being present. The leaf-traces, running out from the primary xylem, are double, traversing the secondary zone almost horizontally. The secondary wood has the usual Cordaitan structure, with medullary rays one cell thick, but is interesting as showing distinct annual rings. The chief peculiarity of the genus, however, is the extensive primary wood, consisting entirely of endarch strands.

Mesopitys.—This genus was also founded by Dr. Zalesky and is based on the *Araucarites Tchihatcheffi* of Göppert. Like *Caenoxylon*, it is a Permian plant from Siberia; as in that genus annual rings are well marked. The pith is small (*e.g.* 3 mm. in diameter), and here also there are definite strands of primary xylem, though not so largely developed as in *Caenoxylon*. The strands are described by Zalesky as endarch throughout, but Seward, who has re-examined the specimens, is not convinced that this is constant; "in a few cases there may be a small amount of centripetal xylem present." Observations of my own tend to confirm Seward's statement. The leaf-trace, unlike that of *Caenoxylon*, is a single strand, where it passes through the secondary wood. The plant resembles *Calamopitys* (*Eristophyton*) *Beiner-tiana* in the presence of sclerotic nests in the pith, and Zalesky suggests an affinity between the two plants.¹

¹ On *Caenoxylon* and *Mesopitys* see Zalesky, "Études paléobotaniques, 1re Partie, Note prélim. sur le *Caenoxylon Scotti*," St-Petersbourg, 1911, p. 13, and his paper on *Dadoxylon Tchihatcheffi*, above cited; also Seward, *Fossil Plants*, vol. iii. 1917, pp. 293 and 295.

Antarcticoxylon is a genus founded by Prof. Seward on a specimen from the Priestley glacier, in lat. 74° S. The species is named *A. Priestleyi*. The plant is of interest from its occurrence so far south, where it was discovered on Capt. Scott's second Antarctic Expedition. The age is probably Mesozoic and not earlier than the Rhaetic; the fossil was thus considerably later than the others described in this chapter. The secondary wood is of a Cordaitean or Araucarian type, with usually uniseriate rays. There are distinct annual rings, as in the two genera last mentioned. The pith is small, and at its margin there is a fairly broad zone of small, delicate tracheides, with spiral or scalariform markings. The leaf-traces of *Antarcticoxylon* are single.¹

Unpublished observations by Mr. Walton indicate that *Antarcticoxylon* is really a species of *Rhexoxylon* (see above, p. 228).

The stems just considered agree, for the most part, in possessing a distinct primary xylem, whether practically exarch as in *Mesoxylon*, mesarch as in *Parapitya*, or more or less completely endarch as in *Caenoxylon* and *Mesopitya*. In the next genus this is not the case.

Metacordaite.—This genus was founded by Renault in 1896 on a specimen from the Permo-carboniferous of Autun. The pith is continuous, not discoid, and contains large resin-canals near the outside. The wood is radially seriated throughout as in *Cordaite*, and completely endarch, with no primary strands. The secondary wood only differs from that of *Cordaite* in the fact that most of the tracheides bear only a single row of bordered pits. The phyllotaxis was $\frac{3}{8}$; the leaf-trace, in traversing the wood, consists of five bundles, arranged in a V, with the strand of an axillary branch above. The multifascicular trace in this region is a peculiarity, though

¹ A full account of *Antarcticoxylon* will be found in Seward, *Antarctic Fossil Plants*, British Museum (Natural History), 1914, p. 17. See also his *Fossil Plants*, vol. iii. 1917, p. 296.

Prof. Boyd Thomson states that he has found six bundles in the trace of *Cordailes Brandlingii*, also in the wood. There are no annual rings. Renault regarded this stem as transitional between the Cordaiteae and the Conifers, but nearer the latter. The data are, however, insufficient to establish this interesting hypothesis.¹

Hapaloxyton.—This genus is of quite uncertain position, but deserves mention on account of its unique structure. The name means "soft wood," and the great peculiarity of the stem is that its wood consists almost wholly of cellular tissue, only quite a narrow zone, next the pith, containing tracheides. Such a structure is quite unknown among Gymnosperms, though paralleled to a certain extent in floating woods of some Dicotyledons, such as the Leguminosae *Aeschynomene* and *Herminiera*. The pith is large (a Cordaitean character); on its outer border there are two or three layers of spiral and pitted tracheides. All the rest of the wide zone of wood is formed of elongated, square-ended cells, without any trace of pits. The parenchymatous mass is traversed by uniseriate rays. Beyond the wood is a broad zone of beautifully preserved phloem, the numerous sieve-plates clearly shown on the radial walls of the sieve-tubes. At the outer edge of the cortex there is a periderm.

The external surface of the specimen bears numerous small leaf-scars each containing the print of a single leaf-trace strand.

The triarch roots are known. While the primary xylem appears to be normal, the secondary wood, here, as in the stem, consists exclusively of parenchyma.

The excellent preservation seems to preclude any doubt as to the correct interpretation of this remarkable structure. The genus was referred by Renault to the Araucarian Conifers, but a relation to Cordaiteae seems

¹ B. Renault, "Note sur le genre Métacordaite," *Soc. d'Histoire nat. d'Autun*, 1896.

about equally probable. The one species, *H. Rochei*, comes from the Permian of Autun.¹

3. *The Root*.—Mixed with the remains of leaves and branches of *Cordaite*s, silicified specimens of *roots* have also been found ; they agree so well in histological structure with the stem, that there is no reason to doubt the

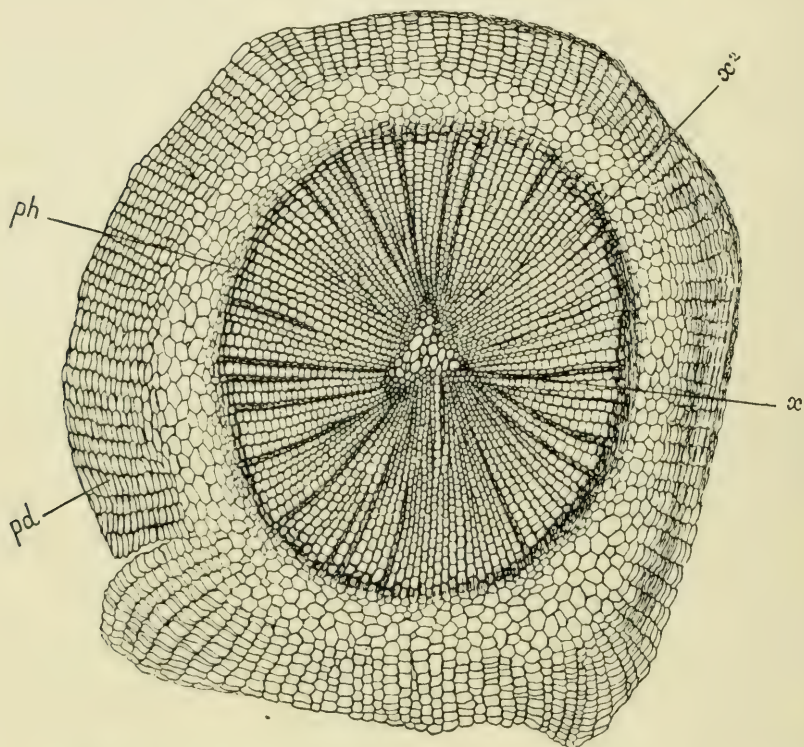


FIG. 105.—*Amyelon radicans* (probably a root of one of the Cordaiteae). *x*, triarch primary xylem ; *x*², secondary xylem ; *ph*, phloem ; *pd*, periderm. \times 23. S Coll. 450. (G. T. G.)

correctness of Renault's conclusion, that they belonged to the same plants, though I am not aware that roots showing structure have yet been found in actual connection with the stem. In the French specimens the roots are diarch, with a broad zone of secondary wood. The elements of the protoxylem are spiral, the rest of the primary tracheides scalariform, while the surrounding

¹ Renault, " Bassin houiller et permien d'Autun et d'Épinac," *Flore fossile*, ii. p. 360, pl. lxxvi.

secondary zone is made up of pitted tracheides and medullary rays, and agrees in all essential respects with the wood of the stem. The root is limited on the outside by a broad zone of periderm, which, from Renault's description, would appear to have been derived from the external cortex. This is unusual in Gymnospermous roots, and the point seems to deserve further investigation.

Our Fig. 105 is taken from a root known as *Amyelon radicans*, frequent in the Lower Coal-measures of England, which in all probability belonged to some member of the Cordaiteae. All the tissues, both primary and secondary, are well preserved. In this case the roots are usually triarch—sometimes tetrarch; in other respects there is sufficient agreement with the French specimens, to leave little doubt as to the affinities of our fossil. In *Amyelon*, at any rate, the origin of the periderm was, no doubt, deep-seated, the cortex being exfoliated. The same was the case in a diarch root associated with a Cordaitean stem, provisionally named *Cordaites shorensis*, from Shore.

4. *The Leaves*.—The leaves of *Cordaites* are fossils of frequent occurrence, especially in the Upper Coal-measures, as, for example, at Radstock in Somersetshire, and in the coal-fields of Central France, where they appear to have played an important part in the formation of coal. At St. Etienne, certain beds of coal are said to consist exclusively of dense masses of the carbonised leaves of Cordaiteae. But in addition to the carbonised remains and impressions, which are ill adapted for the investigation of structure, petrified specimens also occur. Thus, in the "black flints" of Grand Croix, silicified remains of Cordaitean leaves are packed together in layers, "like damp Beech-leaves on the ground in our forests."¹ These silicified specimens are often in a

¹ Solms-Laubach, *Fossil Botany*, English edition, p. 105.

state of exquisite preservation, and rendered it possible for the French palaeontologists, notably Renault, to work out the structure in great detail. The anatomical specimens recorded from France are all referred to the genus *Cordaite*s, though there is often some doubt as to the particular species (as determined from impressions) to which they belonged.

Broadly speaking, the structure of the leaf of *Cordaite*s resembles that of a single pinna of the leaf of a Cycad, such as *Zamia*, while there is a more general resemblance to the leaf of *Agathis*, or one of the larger-leaved *Araucarias*. There are, as might be expected, appreciable specific differences among the various Cordaitean leaves examined. For example, in the leaf shown in transverse section in Fig. 106, A, referred provisionally to *C. angulosostratus*, each of the numerous parallel vascular bundles is enclosed in a strong sheath, which abuts, above and below, on a hypodermal strand of fibres. Smaller hypodermal ribs are interposed between the vascular bundles. The bundle-sheaths are connected together laterally by transverse bridles of thickened cells, which may perhaps be compared to the accessory transfusion-tissue which occurs in the genus *Cycas*.¹ In this species of *Cordaite*s, the mesophyll shows little differentiation. The most interesting point is the structure of the bundles themselves, which agree exactly with those in the leaves of recent Cycads. The xylem is in two parts, with the spiral elements (*t*) between them. The larger portion is towards the upper surface (centripetal, *a*), and the smaller towards the lower surface (centrifugal, *b*). Below this again is the phloem, usually ill preserved. In a word, we have in these cases (Fig. 106, A and C) the collateral, mesarch structure, characteristic of the

¹ A reticulate system of thick-walled tracheides, which extends from the midrib to the margin of the leaflet in this genus. See Worsdell, "On Transfusion-Tissue," *Trans. Linn. Soc.* 2nd ser. (Bot.), vol. v. 1897, p. 308.

bundles of Cycadean leaves, and already familiar to us in other fossil plants. Some other species show the same structure of the bundles, but in several the centrifugal part of the xylem is absent, as in the petioles of

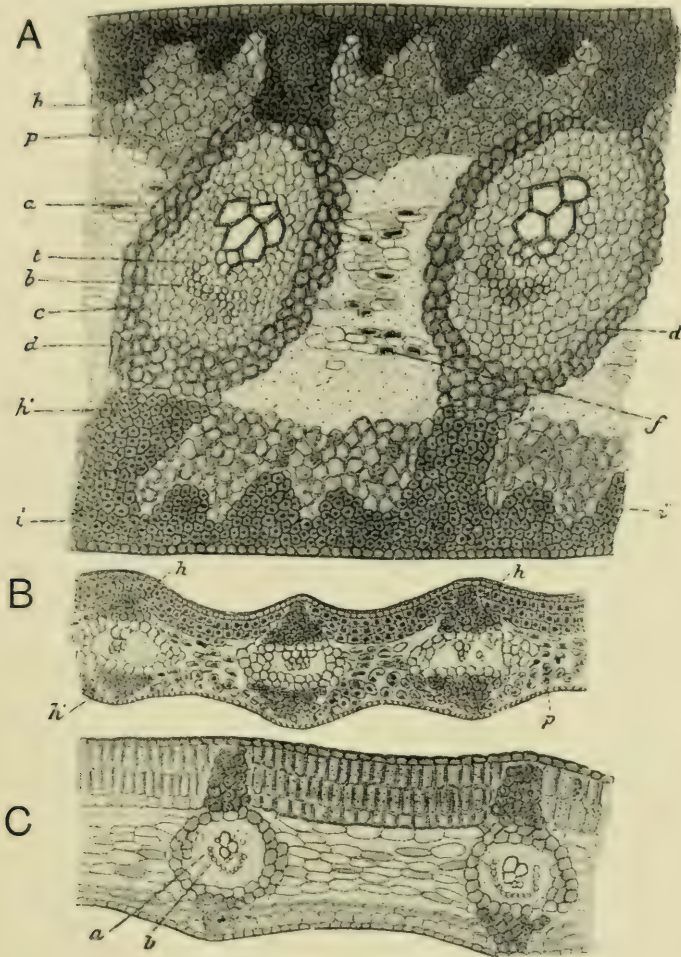


FIG. 106.—*Cordaites*. Leaves in transverse section. A. *C. angulosostriatus* (?). *h, i*, hypodermal ribs of sclerenchyma; *p*, mesophyll; *d*, bundle-sheath; *a*, centripetal xylem; *t*, protoxylem; *b*, centrifugal xylem; *c*, phloem; *f*, tissue connecting the bundles. $\times 60$. B. *C. rhombinervis*. Here the ribs of sclerenchyma only occur in connection with the bundles; palisade-tissue and spongy parenchyma are differentiated. $\times 50$. C. *C. lingulatus*. Ribs as in B; palisade-tissue well marked. $\times 50$. All after Renault.

Medullosa, whereas it only dies out in the finer bundles in the case of recent Cycadean leaves.¹

¹ See M. C. Stopes, "On the Leaf-Structure of *Cordaites*," *New Phytologist*, vol. ii. 1903, p. 91.

In other anatomical points there is considerable diversity of detail. The mesophyll is in some forms clearly differentiated into an upper palisade layer, and a lower lacunar portion (see Fig. 106, B and C). This is beautifully shown in a species investigated by Dr. Marie C. Stopes, and identified as *C. principalis*. In the same species Dr. Stopes observed the very interesting fact that both the inner and outer sheaths surrounding each bundle consist of elements with bordered pits, and may thus be regarded as forms of transfusion-tissue. Otherwise, centrifugal xylem is absent in this leaf. In certain cases the hypodermal ribs are limited to the upper and lower surfaces of the bundles, not occurring between them. In one form (*C. crassus*) the leaf had a distinctly fleshy character, as if adapted to xerophytic life. Numerous stomata, of normal structure, occur in these leaves, on the epidermis of the lower surface, to which they seem to be limited. The general conclusion to which we are led is that, while the leaf, in its simple form and general structure, approaches most nearly to that of such Conifers as *Agathis*, in the details of internal organisation it agrees more closely with a single leaflet of a Cycad, thus showing a striking combination of characters, such as we have already met with in the leaf of *Poroxylon*.

In a large bud, referred to *Cordaites lingulatus*, Ren. (cf. Fig. 99), Lignier was able to follow the differentiation of the tissues in the successive young leaves, an observation rarely possible in a fossil plant. The phloem appeared to be completed early, but the first definite differentiation in the procambial strand is that of the protoxylem; the rest of the centripetal wood follows, and this may be completely formed before the arc of centrifugal xylem becomes lignified. Thus the course of development is quite normal. The bundle-sheath, which bears somewhat irregular bordered-pits on its walls, becomes marked out almost simultaneously with the protoxylem,

while the transfusion tracheides, lying between the sheath and the xylem, are completed about the same time as the centrifugal arc. A secretory gland, probably cellular, not intercellular, is developed early, on each side of the sheath, to which it belongs.

The fibrous bands of the leaf appear as early as the procambial strands, and their cell-walls become thickened concurrently with those of the xylem of the bundles. The differentiation of the palisade and spongy tissues of the mesophyll takes place somewhat late in the development.¹

It has already been mentioned that the leaves, commonly attributed to *Cordaite*s, which occur in the Lower Coal-measures of England, probably belong to the genus *Mesoxylon*, of which the stems are far commoner at such horizons than those of the true *Cordaite*s. Considerable interest therefore attaches to Dr. Margaret Benson's account of a type of leaf named by her *Cordaite Felicis*, occurring frequently in the coal-balls which yield the stems of certain species of *Mesoxylon*. It does not differ in any essential respect from the well-known leaves of *Cordaite*s, but shows definite distinctive characters. The chief feature is that the sclerenchymatous bands placed midway between the bundles extend right through the leaf from one surface to the other, forming regular partitions as seen in transverse section. Additional fibrous bands are present in a hypodermal position. The palisade and spongy tissues of the mesophyll are not strongly differentiated. Each bundle is surrounded by a thick sheath; the walls of the sheath-cells are pitted. As usual, the centripetal xylem forms the chief part of the wood, but where the bundle is fully developed there is a well-marked band of centrifugal xylem. In addition, there are some tracheides between the xylem and the sheath, which may be called transfusion tissue and

¹ O. Lignier, "Différentiation des tissus dans le bourgeon végétatif du *Cordaite lingulatus*," *Ann. des Sci. nat. (Bot.)*, sér. 9, t. xvii. 1913.

represent the inner sheath described by Dr. Stopes in other species. Towards the edges the bundles are somewhat simplified, the centrifugal xylem disappearing, though some transfusion tissue remains. In this, as in other respects, there is a close agreement with the structure of the pinnae in recent Cycads.

Dr. Benson's species agrees very nearly with *C. Wedekindi* and other species described by Felix from the Coal-measures of Westphalia. The nomenclature presents some difficulties, as we can hardly continue to use the generic name *Cordaites* for leaves which in all probability belonged to another genus. At the same time, it is not yet possible to refer Dr. Benson's specimens to a definite species of *Mesoxylon*. The name *Mesoxylon Felicis* might be provisionally adopted for this form of Cordaitean leaf.¹

5. *The Fructifications*.—We now come to the most interesting point in our present subject—the reproductive morphology of the Cordaiteae. The general arrangement and external appearance of the inflorescences have already been described. Our knowledge of these organs has been built up by the labours of successive observers, notably Carruthers, Grand'Eury, Renault, and, more recently, C. E. Bertrand. It is to Renault that our acquaintance with the intimate structure of the flowers is chiefly due, for he was so fortunate as to find silicified specimens, allowing of minute structural investigation, which were clearly of the same nature as the catkins found on the branches of the Cordaiteae. As, however, the petrified fructifications could not be referred with certainty to the particular members of the family to

¹ See M. Benson, "*Cordailes Felicis*," *Ann. of Bot.* vol. xxvi. 1912, p. 201. The measurements in this paper require to be multiplied by ten. Compare Felix, "*Untersuch. über den inneren Bau westfälischer Carbonpflanzen*," *Abh. d. K. Geolog. Landesanstalt*, Berlin, Bd. vii. 1886, p. 61.

which they belonged, the generic name *Cordaianthus* was applied to them, and is still used, as a matter of convenience.

A. *The Male Fructification*

The specimen shown in longitudinal section in Fig. 107, and known as *Cordaianthus Penjoni*, Renault, is a single male catkin,¹ corresponding to one of those which are represented in their external aspect in Fig. 99, borne laterally on the peduncles. The catkin (about a centimetre in length) consists of a rather thick axis, bearing spirally arranged bracts, between which the stamens (using the word provisionally) are inserted (Fig. 107, A). The stamens are either isolated, each in the axil of a bract, or are grouped, two or three together, around the apex of the catkin. Each stamen consists of a filament, surmounted by three, four, or more ² long, vertical pollen-sacs. The filament is traversed by a vascular bundle, which sends a branch to the base of each pollen-sac (Fig. 107, B, g). Some of the sacs in Renault's specimens had already undergone dehiscence, by a longitudinal opening (Fig. 107, B, e); others are preserved intact, and are still filled with the pollen-grains (e'). The wall of each pollen-sac consists of a single layer of cells (Fig. 107, B). In other species (e.g. *C. Saportanus*) the stamens are limited to the apical region of the catkin, and are fewer in number, with shorter filaments.

The morphology of these male catkins of *Cordaites* is open to various interpretations. Renault regarded the male "flower" as consisting of a group of two or three stamens at the apex of the catkin, but as reduced to a single stamen where the position is axillary. Solms-

¹ The word *catkin* is used, rather than cone, to avoid any assumption of homology with the male cone of the Coniferae.

² Renault gave the number as three or four, but, as pointed out by Solms-Laubach, the transverse section shows five or six sacs to each stamen.

Laubach preferred to regard each of Renault's "stamens" as itself constituting a male "flower," the stalk on which the pollen-sacs are borne thus representing a pedicel, and not a filament, while the pollen-sacs are themselves the stamens. On this view there would be a certain resemblance to the male flowers of Gnetaceae. In *Gnetum*, for example, the male flower consists of a stalk

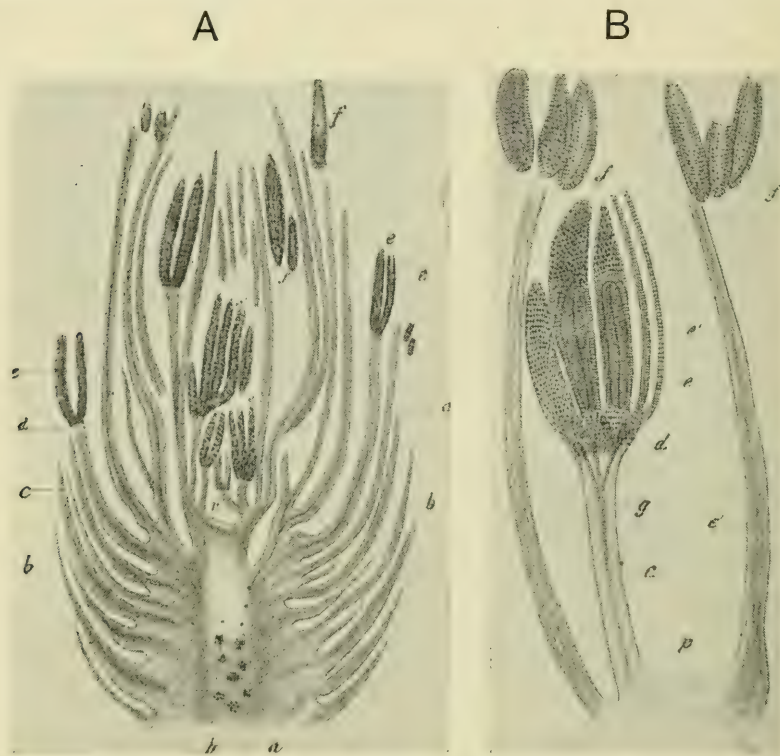


FIG. 107.—*Cordaianthus Penjoni*. A. Longitudinal section of male catkin. a, axis; b, sterile bracts; c, filament, bearing the pollen-sacs (e) at the top; d, junction of filament with pollen-sacs; f, detached pollen-sac; v, apex of axis, with stamens around it. $\times 6\frac{1}{2}$. B. Stamens, more highly magnified. g, vascular bundle of filament, sending branches to the pollen-sacs; e, pollen-sac after dehiscence; e', sac still full of pollen; p, apex of axis. Other letters as in A. $\times 23$. Both after Renault.

bearing two pollen-sacs, each of which is considered to represent a sessile stamen. In *Ephedra* the arrangement is similar, but the sessile stamens vary in number, according to the species, from two to eight, and each consists of two pollen-sacs. The Gnetaceae, however, are a highly modified group, as to the geological history of which we have no certain information. We must be

cautious in using their morphology (which in itself is none too clear) to explain that of an ancient family like the Cordaiteae, which flourished in the Carboniferous period. If, as has been suggested, the flowers of the Gnetaceae are reductions from a much more complex type like that of the Bennettitales (see Chap. V.) it is clear that the family can have only the most remote affinity with the Cordaiteae.¹

Renault's summary of the morphological conditions in the male *Cordaianthus* certainly has the merit of simplicity. He said: "In the midst of sterile bracts arose one or more fertile bracts, the filament of which, scarcely modified, bore at its summit three or four sacs containing the pollen."² On this view, the stamens would in no case be axillary structures, but would represent so many sporophylls, interspersed among sterile bracts. We might compare each stamen to that of *Ginkgo*; in the latter the pollen-sacs are usually only two in number, though stamens with three or four sacs sometimes occur, and are pendulous instead of erect; these differences, however, are of trifling importance. The male catkin of *Cordaianthus* would thus chiefly differ from that of *Ginkgo*, in the presence of sterile bracts among the sporophylls, a difference comparable to the relation which we find, in a remote family, between the strobilus of a *Calamostachys* and that of a recent *Equisetum*. The data, however, are insufficient to justify any definite conclusion as to the exact morphology of the male *Cordaianthus*. It is quite clear, at any rate, that its structure is totally distinct from that of the male cone of a Cycad, and very different from that of a Conifer, or from the male inflorescence of Gnetaceae. On the whole, *Ginkgo* affords perhaps the best parallel. The stamens of the

¹ See Arber and Parkin, "Studies on the Evolution of the Angiosperms: the Relationship of the Angiosperms to the Gnetales," *Ann. of Bot.* vol. xxii. July 1908, and the papers there cited.

² Renault, *Tiges de la flore carbonifère*, p. 308.

Araucarieae with their numerous pendulous pollen-sacs also offer some analogy.

The pollen-grains of *Cordaianthus* were rather large, measuring, in some examples studied by Renault, $\cdot 09 \times \cdot 05$ mm., their form thus being ellipsoidal. The outer membrane had a rather rough surface; in the interior of the pollen-grain, a small group of cells (prothallus or antheridium) can often be detected (Fig. 109, C), an important observation, to which we shall return when speaking of the phenomena of pollination.

B. *The Female Fructification*¹

Renault found that the young female catkins of *Cordaïtes* were scarcely to be distinguished from the male by external characters, though somewhat more globular in form. In the early stages, the ovules were completely hidden by the overlapping bracts. Here also, sections of the silicified specimens have revealed the internal organisation. In a fructification, to which the discoverer gave the name of *Cordaianthus William-soni* (Fig. 108, A), the axis bore numerous, spirally disposed bracts, most of which were sterile, while in the axils of some of them the ovules (*c*) were borne. Each ovule was situated at the end of a very short lateral stalk (*d*), which according to Renault bore some bracteoles; a transverse section of a similar fructification showed four ovules. The supposed bracteoles are of extremely doubtful nature, and Bertrand with good reason considered that they had been wrongly interpreted.

The ovule has a single, thick integument, as was shown by Bertrand. At a later stage the inner layer of the integument became hard and resistant, the outer remaining fleshy. In the middle was the nucellus (Fig. 108, B, *g*, *n*) (somewhat shrivelled in the specimen figured),

¹ See C. E. Bertrand, *Le Bourgeon femelle des Cordaïtes, d'après les préparations de Bernard Renault*, Nancy, 1911.

the upper part of which contained the pollen-chamber. A vascular bundle entered the chalaza, and sent out two

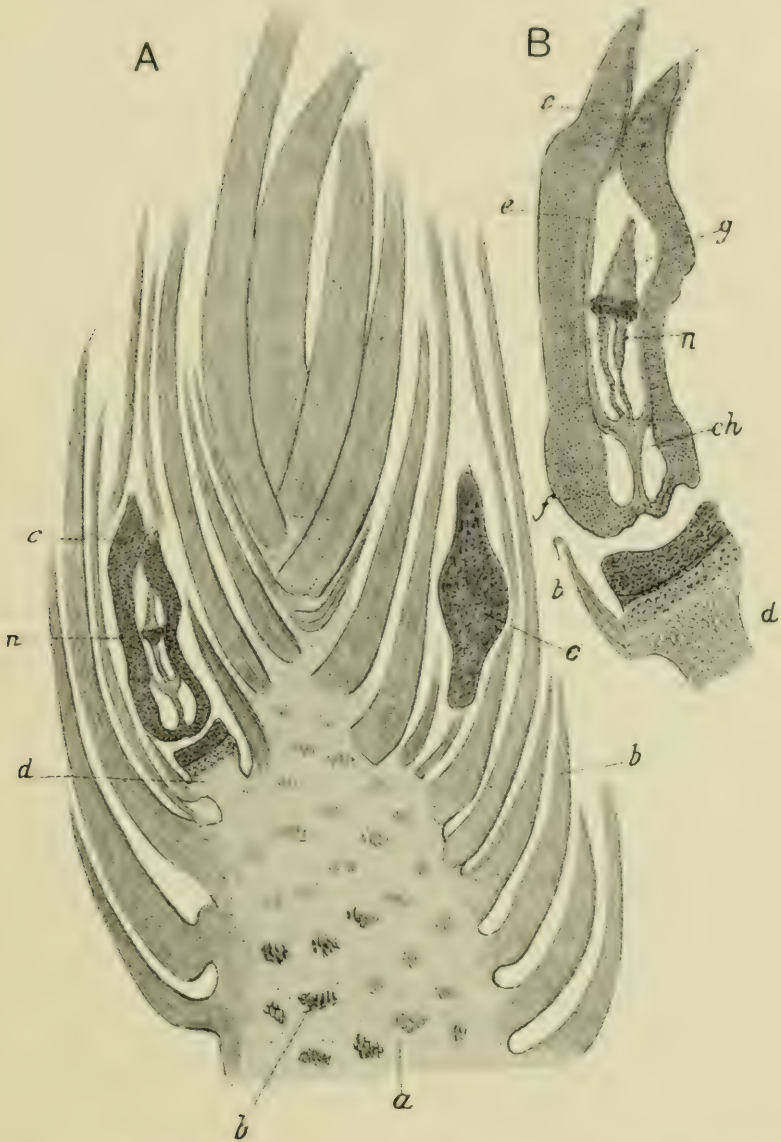


FIG. 108.—*Cordaianthus Williamsons*. A. Somewhat tangential section of a female catkin, showing two ovules. *a*, axis; *b*, sterile bracts, and bundles running to them; *c*, ovules; *d*, axillary pedicel, bearing an ovule; *n*, nucellus. \times about 10. B. Ovule, more highly magnified. *d*, short pedicel, terminated by the ovule; *b*, supposed bracteole; *c-f*, outer, *e*, inner layer of integument; *ch*, chalaza; *n*, shrivelled nucellus; *g*, apex of nucellus. \times about 35. After Renault.

branches into the integument, and no doubt others into the nucellus.

Further details were worked out in a fructification, specifically distinct, named *Cordaianthus Grand'Euryi* by Renault. Here the axis, apparently terminated by the ovule (shown detached in Fig. 109, A), bore several bracts. The integument is broken and displaced, leaving the nucellus nearly isolated in the middle of the ovule.

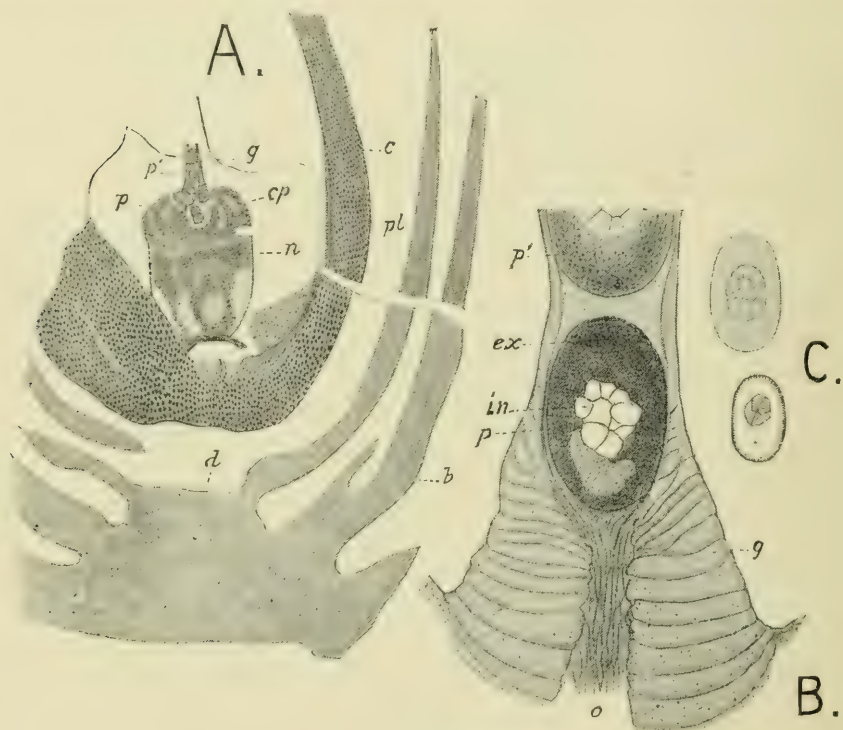


FIG. 109.—*Cordaianthus Grand'Euryi*. A. Longitudinal section of female catkin, showing one ovule, just pollinated. *d*, axis; *b*, bracts; *c*, integument; *n*, nucellus; *cp*, pollen-chamber; *g*, canal of pollen-chamber; *p*, pollen-grains in chamber, and *p'*, in canal. $\times 24$. B. Canal of pollen-chamber enlarged. *g*, dilated cells, enclosing the canal, *o*; *p*, *p'*, two pollen-grains in the canal; *ex*, outer membrane of pollen-grain; *in*, group of prothallial or antheridial cells within the grain. $\times 150$. C. Grains of pollen, showing internal cells; the smaller grain from an anther, the larger from the canal of an ovule. \times about 100. All after Renault.

In the upper part of the nucellus, we see the pollen-chamber (*cp*), surmounted by a very curious neck, shown, on a large scale, in Fig. 109, B. Both in the pollen-chamber itself and in the canal leading to it, pollen-grains (*p*) are contained, so that this ovule, as Renault said, was "surprised at the very moment of pollination." The wall of the canal has a characteristic structure, for the

cells in its lower part are transversely elongated, so as to partially close the passage (Fig. 109, B, g). Possibly this may have been an arrangement for shutting the entrance to the pollen-chamber after pollination had been effected.

The pollen-chamber is, as we have already seen (Chap. I. p. 68, and Chap. III. p. 206), a general feature in Palaeozoic seeds. The pollen-chamber of *Trigono-*

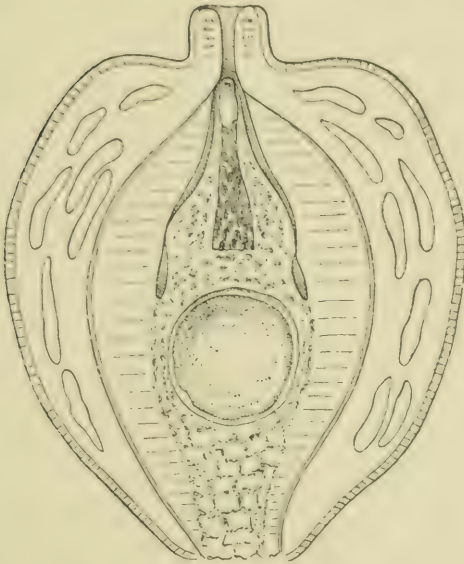


FIG. 110.—*Cycas*, sp. Longitudinal section of ovule, showing the thick double-layered integument enclosing the nucellus. The round body in the lower half of the nucellus is the embryo-sac; the flask-shaped cavity in the upper part is the pollen-chamber containing pollen-grains. From Griffith, 1852.

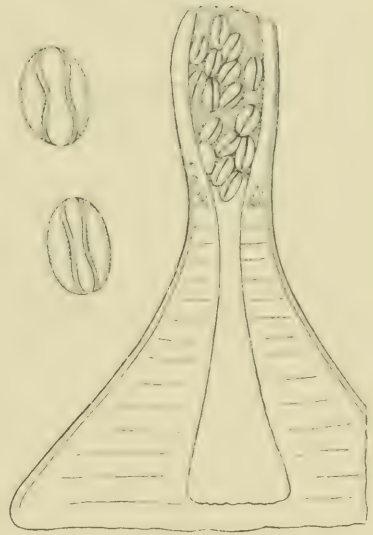


FIG. 111.—Pollen-chamber enlarged, showing pollen-grains in the canal. Two pollen-grains, further enlarged, on the left. From Griffith, 1852.

carpus, for example, among the Pteridosperms bears a rather close resemblance to that of a Cordaitan seed (see Fig. 79, p. 205). The Cycadaceae and *Ginkgo* are the only recent plants in which this organ is known; the pollen-chamber of *Cycas* was originally discovered before the middle of the last century by our countryman Griffith, who gave excellent figures of it, which are here reproduced¹ (Figs. 110, 111). Many

¹ Griffith, *Icones Plant. Asiat.* Part iv. Pl. 377 and 378, 1852. *Notulæ ad Plant. Asiat.* pp. 6-8, 1854. Both these works were posthumous; Griffith died in 1845.

years later it was rediscovered independently by De Bary and Brongniart, both of whom were unaware of Griffith's observations.

The pollen-grains in the canal and pollen-chamber of the ovule of *Cordaïtes* are larger than those still contained in the anther, and their internal group of cells is more developed (Fig. 109, C); grains, which were found lying free in the matrix, were in an intermediate condition; Renault drew the conclusion that the pollen-grains continued to grow after their discharge from the anther, and more especially after their entrance into the pollen-chamber.

The cells within the pollen-grain of *Cordaïtes* are more numerous than in most recent Gymnosperms; in the pollen-tube of *Microcycas*, however, described by Caldwell,¹ sixteen spermatozoids are produced, while in that of *Araucaria* the number of nuclei present ranges from about twenty to forty-four.² In the pollen-grains of *Cordaïtes*, as Renault pointed out, the cells appear to have been all of one kind. That this structure, whether it be regarded as a prothallus or as an antheridium, should have been more developed in primaeval seed-plants than is usual in those of our day, is quite what we should expect, from our knowledge of the analogous conditions in the heterosporous Cryptogams.³

Pollen-grains have now been observed, in a number of instances, within the pollen-chambers of Pteridospermous and Gymnospermous seeds of the Carboniferous period. There appears to be little or no evidence at present for the formation of pollen-tubes, though the preservation is sometimes good enough for even so delicate a structure to have been detected. It is probable that such pollen-grains as those of *Cordaïtes* or

¹ "*Microcycas calocoma*," *Bot. Gazette*, vol. xlv. 1907, p. 118.

² Lopriore, "Über die Vielkernigkeit der Pollenkörner von *Araucaria Bidwillii*," *Ber. d. Deutsch. Bot. Gesellschaft*, vol. xxiii. 1905, p. 335.

³ See the account of *Stephanospermum* above, p. 209.

Stephanospermum may have been rather more like the Cryptogamic microspore than those of *Cycas* or *Ginkgo*, that no pollen-tube was developed, but that the relatively large antheridium at once produced a number of spermatozoids, for we are probably justified in regarding the cellular body within the pollen-grain of *Cordaitea* as an antheridium, rather than as a vegetative prothallus. In the absence of a pollen-tube, the spermatozoids would have needed to be more numerous, for, having a longer distance to cover by their own movements, they would presumably have reached their goal with less certainty. The pollen-tube may probably be regarded as a later adaptation, which served the purpose of economising spermatozoids, and ultimately rendered their motility unnecessary. Even in the Cycads and *Ginkgo*, where the pollen-tube serves mainly as an anchoring and food-absorbing organ, its growth ultimately brings the spermatozoids with much precision to their goal—the necks of the archegonia.¹

Returning to the ovules, it may be mentioned that they are somewhat flattened in the plane tangential to the catkin; the two integumental bundles are placed laterally, one near each edge of the ovule. The integument terminated above in a bi-lobed body, interpreted by Bertrand as an apparatus for collecting the pollen. A certain number of the ovules in a catkin seem to have been abortive.

The flattened ovule of *Cordaianthus* was evidently destined to develop into a platyspermic seed. Bertrand found that the structure agrees most closely with seeds of Brongniart's genus *Diplotesta*, which is nearly allied to *Mitrospermum*, a seed described below.

The organisation of the catkin bearing the ovules was worked out in detail by Bertrand. The axis, which is completely clothed by the bases of the bracts, contains

¹ See, for example, Webber, *Spermatogenesis and Fecundation of Zamia*, U.S. Dept. of Agriculture, 1901, p. 63.

a vascular ring of about ten isolated strands. Each bract receives a single bundle, described as identical with one of the nerves of the vegetative leaf of *Cordaites*. The free bract is strengthened by hypodermal bands of fibrous tissue. It will be remembered that the catkins are borne on a naked stalk, forming the main axis of the inflorescence (see Fig. 99).

Mesoxylon.—Until recently nothing was known as to the structure of the fructification in the Cordaiteae of the British Coal-measures, though various impressions referred to *Cordaianthus* had been described. There is now, however, good evidence that the axillary shoots of *Mesoxylon multirame*, already mentioned, were the inflorescence of that plant. These shoots, as they appear in the axils of the leaves, are naked, somewhat fleshy organs. Free specimens show the general structure of the whole shoot. It is bilaterally symmetrical, consisting of a leafless main axis, containing a flattened stele and bearing distichously arranged bud-like branches, lying in the plane of the major axis of the main shoot. Each branch or bud bears numerous spirally arranged bracts of strong, mechanical construction (see Fig. 112, which shows the main axis and one of the buds). As regards the anatomy of the bud, it possesses a ring of vascular strands, from which each bract receives a single leaf-trace, of mesarch structure.

The morphology of these shoots is identical with that of various species of *Cordaianthus*, described by Grand'Eury in 1878. The main axis of the inflorescence is described by him as fleshy and as a "naked peduncle." He laid stress on the distichous arrangement of the buds on the axis, saying that "the distichous arrangement of the buds is the sign of a new destination," *i.e.* of their reproductive function. The buds and their bracts agree closely in organisation and structure with the catkins of *Cordaianthus*, minutely described by Bertrand. It thus appears to be proved that the peculiar axillary

shoots of *Mesoxylon multirame* constitute the *Cordaianthus* of that species.

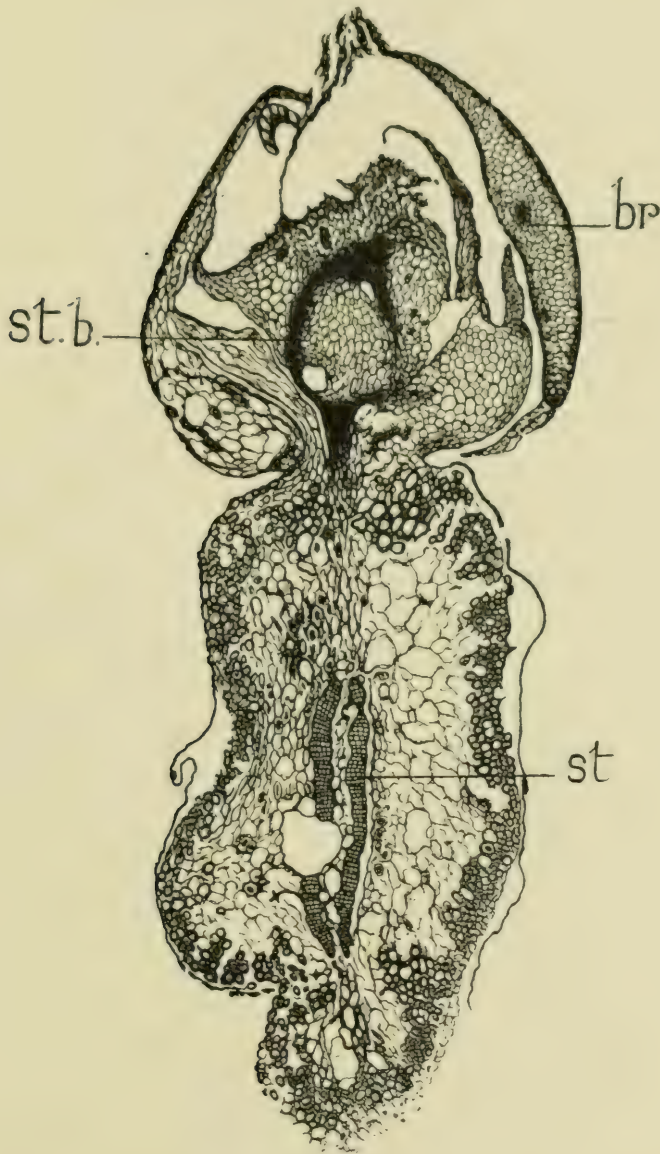


FIG. 112.—*Mesoxylon multirame*. Somewhat oblique transverse section of a fertile shoot, showing a bud or catkin attached to the main axis of the inflorescence. *st*, stele of axis; *st.b.*, stele of bud; *br*, a bract of the bud. \times about 15. S. Coll. 3040. (G. T. G.)

The sex of the *Mesoxylon* inflorescence could not be determined for certain, as neither stamens nor ovules are preserved *in situ*. Renault speaks of the bracts of

the female catkin as thicker and more coriaceous than those of the male. This points to the *Mesoxylon* catkins having been female, as the bracts are strongly built, and agree exactly with those of the female buds described by Bertrand. Seeds of *Mitrospermum compressum* are associated, but not connected, with the fertile shoots.

It thus appears that the reproductive apparatus of *Mesoxylon*, like the vegetative organs, was constructed on the same plan as that of *Cordaites*.

Morphology.—Former speculations on the morphology of the female *Cordaianthus* have to a great extent lost their basis, in consequence of Bertrand's more accurate observations. The comparison with Gnetaceae no longer has any point, now that the Cordaitean ovule is proved to have possessed only a single integument, and, as the supposed presence of bracteoles on the pedicel of the ovule is now discredited, we can no longer assume that the pedicel represents an axillary shoot; it may merely be the funiculus of the ovule itself.

Taking the facts as they stand, the female catkin may be described as a very simple form of cone, with each megasporangium apparently axillary to a subtending bract, an arrangement for which an analogy can of course be found in the quite unrelated genus *Selaginella*. The fact that most of the bracts are sterile is, however, remarkable, and another peculiar feature is the great elongation of the mature pedicel in various fructifications referred to *Cordaianthus*. Such cases may suggest a vague analogy with *Ginkgo*, but the pedicel of *Cordaianthus* never bears more than one seed, and if it is an axillary shoot there is nothing to represent the carpel. The data are, in fact, insufficient for the interpretation of the female catkin in terms of any recent Gymnospermous fructifications. We can only say that the indications of affinity point towards Coniferae or Ginkgoales rather than towards Cycads, with which the Cordaiteae seem to have little in common, so far as the fructifications,

apart from the seed itself, are concerned. We must, however, remember that our living Cycadaceae only represent one or two special surviving groups of a class once vastly more extensive and varied. The possibility of a comparison between the reproductive morphology of the Cordaiteae and that of the Mesozoic Bennettitales (Chapter V.) has been maintained by some botanists, though on inadequate grounds.

The highly specialised inflorescences of the Cordaiteae, whether male or female, are clearly as remote as possible from the simple fructifications of the Pteridosperms, in which, so far as we know, both pollen-sacs and seeds were borne on portions of the frond differing but little from the vegetative foliage. There is a wide gap here, though in other respects, especially in the structure of the seeds themselves, a certain affinity between the two groups is plainly manifested.

6. *The Seeds*.—In some cases seeds, in a more or less ripe state, have been found attached to the inflorescence, and in connection with the leafy twigs of Cordaiteae. These seeds sometimes appear to have been solitary, a single seed representing the female catkin as above described. This may indicate a real morphological difference, like that between *Taxus* or even Ginkgoaceae and the Coniferae with true cones, but it may be equally well explained if we suppose that only one ovule in each catkin developed into a ripe seed. In some specimens, as in *Cordaianthus anomalus*, Carruthers, each seed was seated on a long slender stalk or peduncle; ¹ this may have been developed during the ripening of the seed. Our knowledge of the comparative morphology of the Cordaiteae has unfortunately made little progress in recent years, owing to the want of adequate material.

In certain cases, the seeds found in connection with

¹ Carruthers, "Notes on some Fossil Plants," *Geol. Mag.* vol. ix. 1872.

the inflorescences of *Cordaites* have a characteristic cordate form. This has rendered it possible to identify, with great probability, a certain number of the isolated seeds as belonging to this family. Such direct evidence is very necessary, for, as we have already seen (Chaps. I. and III.), a large number of the Palaeozoic seeds belonged to Pteridospermeae, and, where they were of the platyspermic type, may be extremely difficult to distinguish from those of Cordaiteae. It is also probable that the seeds of primitive Coniferae and Cycadophyta (both of which groups already existed, at least in the later Palaeozoic times) may be represented among the detached seeds. We will first describe a type of seed which is known, from the evidence of attached specimens, to have been produced by the Cordaiteae, and was therefore named *Cordaicarpus* by Renault,¹ though the old name *Cardiocarpus* is now reinstated.

These seeds are heart-shaped at the base, and somewhat flattened, being of the platyspermic type. The testa is double, the outer envelope, or sarcotesta, having been soft and fleshy during life, while the inner layer, or sclerotesta, was hard and lignified. Renault regarded the two layers of the testa as having been derived from two integuments, a view for which there is no sufficient evidence. So in the case of recent Cycadaceous seeds, some botanists have regarded the double testa as representing two integuments, while others, with better reason, consider that a single integument has undergone differentiation into distinct layers.

The vascular bundle which enters the chalaza gives off branches, both into the testa and into the nucellus ;

¹ These seeds were originally named *Cardiocarpon* and subsequently *Cardiocarpus* by Brongniart, a name used by Carruthers and Williamson in the form *Cardiocarpon*. As pointed out in Vol. I. Chapter VI. (p. 175), certain "seeds" referred by Williamson to *Cardiocarpon* really belonged to Lycopods and are now named *Lepidocarpon*. A valuable account of seeds referred to Cordaiteae will be found in Seward's *Fossil Plants*, vol. iii. chap. xxxv., iii. *Cardiocarpales*.

the former traverse the inner part of the sarcotesta, a double bundle running up on each side of the seed, just outside the lateral edges of the sclerotesta (cf. *Rhabdocarpus*, Fig. 92), while the latter enter the nucellus and traverse its tissue. At its micropylar end, the nucellus, which was probably free from the integument, contains a pollen-chamber, provided with a neck, which projects into the micropyle. Apart from its bilateral symmetry, the seed agrees very nearly in structure with the *Trigono-*

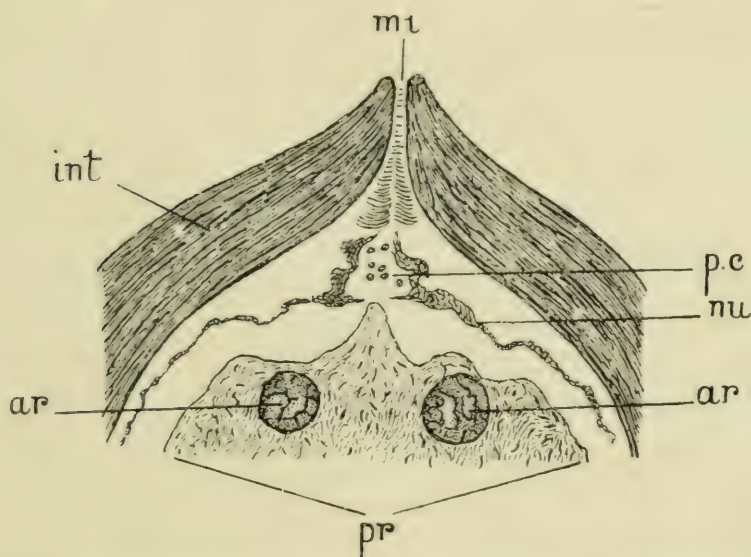


FIG. 113.—*Cycadinocarpus angustodumensis*. Upper part of seed, in longitudinal section. *int*, integument; *mi*, micropyle; *nu*, remains of nucellus; *p.c.*, pollen-chamber, containing pollen-grains; the chamber has a long neck or canal, extending up into the micropyle; *pr*, endosperm; *ar*, archegonia. Magnified. After Renault.

carpus type, described on p. 204. In certain species of *Cardiocarpus* the archegonia have been found. They occur in the usual position, at the upper end of the endosperm, and two of them are shown in a longitudinal section of the seed.

Our illustration, Fig. 113, is from a seed which Renault and Bertrand separate generically from *Cardiocarpus*, on account of the distribution of the vascular bundles. In *Cycadinocarpus*, as the genus is named, the inner vascular system follows the endotesta, and does not enter

the nucellus, a course which resembles that in the seeds of recent Cycads, with the exception of *Bowenia*. The outer bundles are given off from the chalazal strand after it has entered the sclerotesta, and not below it, as in *Cardiocarpus*. In other respects the seed agrees with *Cardiocarpus*. Two archegonia (*ar*), spherical in form, are clearly shown; between them, the endosperm has an upward prolongation, which is interesting, as it exactly corresponds to the structure found in *Ginkgo* at the present day, and compared by Hirase to a tent-pole, supporting the nucellar membrane, which represents the tent. The pollen-chamber (*p.c.*), with its long neck rising up into the micropyle (*mi*; cf. Figs. 110 and 111), contains pollen-grains. Only the sclerotesta (*int*) of the seed-coat is shown in the figure.

A seed, frequent in the coal-balls of the British Lower Coal-measures, was named *Cardiocarpon compressum* by Williamson, but has been placed in a distinct genus, *Mitrospermum*, by Dr. Agnes Arber, who investigated its structure.¹ This seed is closely associated with the fertile shoots of *Mesoxylon multirame* and may have probably belonged to that plant, though the evidence is not decisive.

The diagrams in Fig. 114 and the transverse sections in Fig. 115 will give a sufficient idea of the structure of the seed. It is markedly platyspermic, as the specific name implies, and measures, when complete, nearly a centimetre in the principal plane by about 3 mm. in the other direction. In surface view, the seed is somewhat heart-shaped. The sarcotesta forms two extensive wings at the sides and extends above the sclerotesta at the micropylar end. Inside the sclerotesta or shell there are some remains of an "inner flesh" as in the seeds of Cycads. There are indications that the shell may have split into valves when mature.

¹ A. Arber, "On the Structure of the Palaeozoic Seed *Mitrospermum compressum* (Will.)," *Ann. of Bot.* vol. xxiv. 1910.

The distinction from *Cardiocarpus* lies in the course of the bundles supplying the seed. In *Cardiocarpus*, as already mentioned, the lateral integumental strands are given off from the main supply in the sarcotesta, before the shell is reached. In *Mitrospermum* the main bundle passes through a foramen in the sclerotesta before branching, so that the lateral strands have to traverse the base

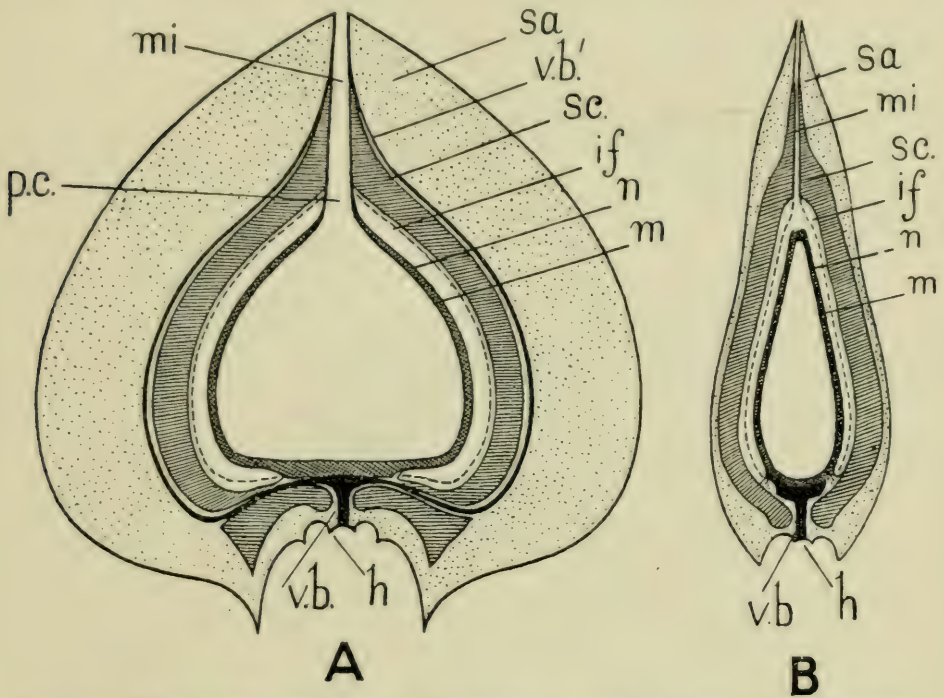


FIG. 114.—*Mitrospermum compressum*. Diagrammatic sections of seed. A, in principal plane; showing the wings. *h*, hilum at base of seed; *v.b.*, main supply-bundle; *m, n*, megaspore and nucellus; *i.f.*, inner flesh; *sc.*, sclerotesta; *v.b.'*, one of the lateral bundles of the integument; *sa*, sarcotesta, forming the wings; *mi*, micropyle; *p.c.*, pollen-chamber. B. In plane at right angles to the former. For lettering see A. After Dr. Agnes Arber, modified to show the micropyle.

of the shell before entering the sarcotesta (Fig. 114, A). They then turn upwards, following the lateral grooves of the shell (see the transverse sections in Fig. 115). Each bundle is much flattened, forming a tracheal plate. There are also tracheides at the base of the nucellus, but whether they extend up into the free nucellus could not be determined.

The nucellus is not well preserved, and the form of

the pollen-chamber is not clear. As the micropyle is approached, however, the nucellus contracts to a small size (Fig. 115, A), and it is probable that the contracted region may be taken as representing the pollen-chamber, for pollen-grains have been found in it. The pollen-grains are elliptical, measuring about $120\mu \times 80\mu$, a size comparable to that of the pollen found in the *Cordaianthus* ovules. In favourable cases, the prothallus filling the megaspore is more or less completely preserved.¹

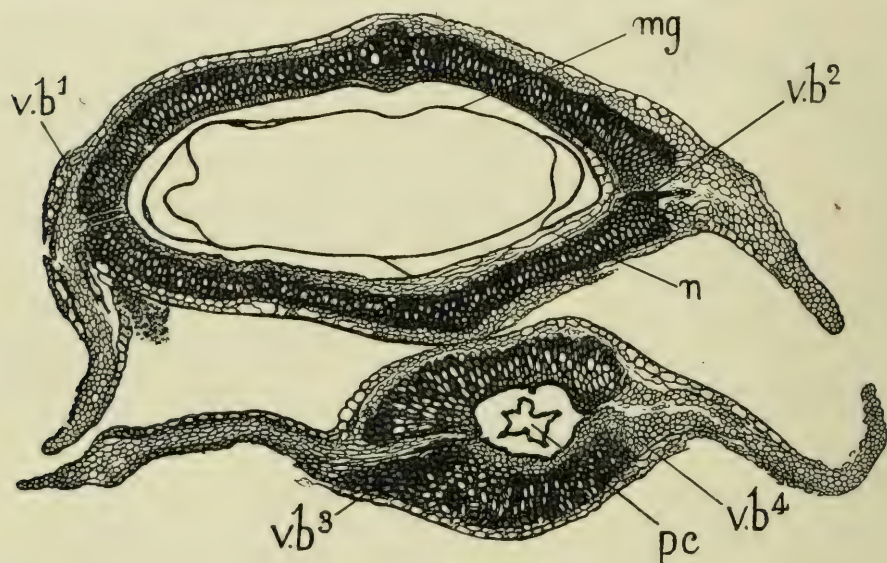


FIG. 115.—*Mitrospermum compressum*. Two seeds lying side by side in transverse section. The upper figure is in section through the body of the seed, the lower about at the base of the micropyle. In both figures the wings are conspicuous. *v.b.*¹, *v.b.*², the lateral bundles in the body of the seed; *v.b.*³, *v.b.*⁴, the same in the micropylar region; *mg*, megaspore membrane; *n*, nucellus; *p.c.* (in lower figure) the pollen-chamber. The sarcotesta and sclerotesta are evident in both figures. \times about 14. S. Coll. 3025. (G. T. G.)

It is evident that *Mitrospermum* is a seed belonging to one of the Cordaiteae, and in all probability to a *Mesoxylon*. It is possible, as Dr. Agnes Arber points out, that more than one species may be embraced under the name *Mitrospermum compressum*.

Diplotesta, the seed that Bertrand regarded as representing the ripened ovule of Renault's *Cordaianthus*, only differs from *Mitrospermum* in small details of structure.

¹ See Scott, 1919, above cited, Pl. ii. Figs. 15 and 16.

Although so many Pteridospermous and Gymnospermous seeds have been discovered in the Carboniferous formation, and often in a wonderful state of preservation, no embryo has, as yet, been found in any of them. The possible explanation of this fact has been discussed in connection with the seed of *Lyginopteris* (see Chapter I. p. 71).

The investigation of the Palaeozoic seeds, which was allowed to rest for some time after the classical researches of Brongniart, Renault, and Williamson, has since been actively pursued, having been greatly stimulated by the discovery of the seeds of the Pteridosperms.¹

7. *Affinities*.—We have now completed our sketch of the principal characters of the Cordaiteae, and may briefly sum up the conclusions to which we are led.

In their vegetative characters, the Cordaiteae hold the balance very evenly between Cycads and Conifers, while at the same time showing much that is peculiar to themselves. The structure of stem and root is, on the whole, very near that of the Coniferae; the secondary wood especially would by itself rouse no suspicions that we had anything but an Araucarian Conifer before us. The large size of the pith in the stem, however, is unlike anything known in Coniferae, and rather suggestive of a Cycad, though in its peculiar discoid structure the pith of some Cordaiteae is quite different from that of Cycads.

The double leaf-trace is a striking point of agreement with *Ginkgo* on the one hand, and with certain of the Pteridosperms on the other; Poroxyleae form a connecting link with the latter in this respect.

The wood of the stem was wholly centrifugal in

¹ An interesting interpretation of the seeds of *Taxus* and its allies, in the light of the seed-structure of Cordaiteae, will be found in B. Sahni, "On Certain Archaic Features in the Seed of *Taxus baccata*, with Remarks on the antiquity of the Taxineae," *Ann. of Bot.* vol. xxxiv. 1920, p. 117.

development, in many of the specimens investigated belonging to undoubted Cordaiteae; but this distinction is not constant, for, as we have seen, there are stems, of true Cordaiteae (*Mesoxylon*), in which centripetal wood is present, as it is in the Poroxyleae and Pityeae. If the seeds of *Poroxylon* are represented, as Grand'Eury believed, by *Rhabdocarpus*, the very close affinity of this family to true Cordaiteae is further confirmed.

The leaves, in their general form and venation, recall those of such Coniferae as *Agathis*, though often greatly exceeding those of any known Conifer in size.¹ In internal structure the leaves agree almost exactly with the single pinnae of the leaf in Cycads.

In general habit, the lofty stem, with well-marked internodes, departs altogether from the ordinary Cycadean type, and much more resembles that of a Conifer, but, in many species, at any rate, the crown, with its abundance of huge simple leaves, must have presented an appearance totally unlike anything in either of the recent families.

It is to the reproductive organs—the male and female fructifications and the seeds—that we naturally attach the chief importance in considering the affinities of the Order. It is just in these organs, however, that we find the most remarkable combination of characters, both such as are common to various other families and such as are altogether peculiar to the fossil group. The stamiferous flowers (however we may interpret them) are very different from anything known to us, either in the Cycadaceae or the true Coniferae. A comparison, though in either case a remote one, is possible with the Gnetaceae (*Gnetum* or *Ephedra*), on the one hand, or with *Ginkgo*, on the other. On the former alternative, we

¹ In *Agathis macrophylla*, from the Queen Charlotte Islands, the leaves attain a length of 17 cm. and a breadth of 5 cm. Seward and Ford, "The Araucariaceae," *Phil. Trans. Royal Soc. B*, vol. 198, 1906, p. 315.

should have to regard the stalked tuft of pollen-sacs as representing an axis, bearing sessile anthers ; on the latter, we should interpret it as a single sporophyll, with terminal microsporangia. The latter view is the simpler, and the analogy with *Ginkgo*, in many respects a primitive type, is more valuable than that with the highly specialised Gnetaceae. On any view, however, the organisation of the male flower of Cordaiteae is quite peculiar and unlike that in other Gymnosperms, and even if it stood alone would serve to mark them as a distinct Order.

The female strobilus, like the male, is as remote as possible from that of the Cycads, but may be better compared with the cone of the Coniferae.

Prof. B. Sahni considers that the Taxales (*Taxus*, *Cephalotaxus*, *Torreya*), as well as *Ginkgo*, are most closely connected with the Cordaiteae. This is, of course, a perfectly tenable view, but the uncertainty as to the morphology of the *Cordaianthus* catkin leaves everything in doubt.

Prof. Sahni further discusses the relation of Cordaiteae to the Pteridosperms, dwelling especially on the important differences between the two groups, both in the fructification and the foliage. He distinguishes between *Phyllosperms*, with leaf-borne seeds (including Pteridosperms and Cycads) and *Stachyosperms*, with stem-borne seeds (including Cordaiteae, Ginkgoales, and all Conifers). It is, however, by no means certain that this distinction holds good. In Cordaiteae, as we have seen, the evidence for the axile nature of the ovular pedicel has been shaken. In Coniferae, if we adopt the placental interpretation of the ovuliferous scale, the seeds are leaf-borne, not stem-borne.¹

The comparison of the female inflorescence with that of the Gnetaceae seems to rest on a very weak basis. There is no longer any ground for believing that the

¹ See Sahni, "On the Structure and Affinities of *Acmopyle Pancheri*," *Phil. Trans. R.S. Ser. B.* vol. 210, 1920, p. 296.

ovule of Cordaiteae had two integuments, still less is there any indication that the two were of a different morphological nature, as appears to be the case in Gnetaceae. It is possible that the affinities of the Gnetaceae may lie in quite a different direction, namely, in that of the Mesozoic Bennettitales (see Chapter V.).

The structure of the seeds which are known to have belonged to Cordaiteae is altogether Cycadean, and, as we have seen, even minute details, such as the form of the pollen-chamber, can be exactly paralleled among recent Cycads. These facts, together with the foliar structure, appear to prove conclusively a real affinity between the two families, though in other respects they diverged widely from one another. But just in the points where there is a strong agreement with Cycadaceae (with Bennettitales the relation, as regards the seed-structure, is much less close) the Pteridosperms are likewise approached. The anatomical characters, together with the seed-characters and those of the multicellular pollen-grain, show such manifest correspondence, that there can scarcely be a doubt that Cordaiteae sprang from the same stock with Pteridosperms, though at a very remote period. The characters which they share with the Cycadophyta are no doubt due to a common origin rather than to any direct connection in later periods.

Returning for a moment to the anatomical characters, it may be pointed out that the general structure of the leaf in Cordaiteae agrees so closely in essential points with that of *Poroxylon*, that we can scarcely doubt that the two groups were nearly allied. *Poroxylon* retained centripetal wood in the stem, a primitive character which some of the Cordaiteae had lost. The Poroxyleae appear thus to combine the characters of Lyginopterideae or Calamopityeae with those of Cordaiteae, though their horizon is too late for us to regard this family as an actual link with the Pteridosperms. The Pityeae belong

to the earliest Carboniferous times, and recent work has shown that they formed a distinct group.

The affinities of the Cordaiteae and of the Cordaitales generally are, as we have seen, extraordinarily complex, and cannot be cleared up until our data are much more extensive than at present. The great step which has been made in the last few years is the full confirmation of the affinity between Cordaitales and the Pteridosperms, which the discovery of the seeds of the latter class has afforded. The relations to Cycadophyta, Ginkgoaceae, and Coniferae have long been recognised, and thus a strong presumption is established that the whole of the Gymnosperms sprang originally from the same ancient stock (see Chapter VI.).

CHAPTER V

THE MESOZOIC GYMNOSPERMS

I. CYCADOPHYTA

OUR studies have so far been almost entirely limited to plants of Palaeozoic age ; in order to carry out our plan of directing attention to discoveries of fundamental botanical importance, we have now to give an account of the Mesozoic Cycadophyta, a group among which some of the greatest triumphs of Palaeobotany have been won.

From the Trias onwards to the Lower Cretaceous, the Mesozoic vegetation maintained, on the whole, a very uniform character, widely different from that of the preceding Palaeozoic period. Throughout the earlier Mesozoic ages true Ferns were abundant, more so, no doubt, than in the preceding period ; Conifers, often much resembling recent types, had become a dominant group, and the family now represented solely by the Maidenhair tree (*Ginkgo*) was of considerable importance. The most striking feature of the vegetation, however, in all parts of the world, was the abundance of plants belonging to the same great class with the recent Cycadaceae, now so limited a group. The Cycadophyta, in fact, were as characteristic of Mesozoic vegetation as are the Dicotyledons of our present Flora. Among the commonest remains are leaves, which in many cases closely simulate those of existing Cycadaceous genera, and have hence received the names *Zamites*, *Dioonites*,

and *Cycadites*. These generic resemblances, however, are usually deceptive; the *Zamites* and *Dioonites* leaves are now known to have belonged to plants which had only a somewhat distant affinity with the Order Cycadaceae, while in certain leaves once referred to *Cycadites*, or even to *Cycas* itself, the similarity to those of the recent genus has proved to be illusory (see below, p. 368). In other leaf-genera, again, such as *Otozamites* and *Anomozamites*, the foliage, while of a Cycadean type, differs evidently from that of any of the existing genera.¹

In addition to the leaves, fossil trunks, which present the external characters of Cycadean stems, are of common occurrence in the older Secondary rocks, as, for instance, in the Wealden of Sussex and in the well-known "dirt-bed" of the Lower Purbeck strata in the Isle of Portland, and at other places along the Dorsetshire coast. The stems are usually short, though they may appear shorter than they actually were, owing to pressure of the super-incumbent strata. The surface is usually covered by the closely-set bases of the leaves; the upper end of the stem is commonly hollowed out, owing to the decay of the growing apex. "Fossil crows' nests" is the name by which such specimens are known to the Portland quarrymen. In certain trunks from the Sussex Wealden, named *Bucklandia* by Mr. Carruthers, an alternation of the scars of foliage and scale leaves has been traced, such as is found in *Cycas* at the present day. These stems, however, are now believed to have belonged to *Williamsonia*, a group quite remote from the recent Cycadaceae (see p. 353). In some cases the stems attained a moderate height, as in *Bucklandia* and the *Cycadeoidea gigantea* of Seward, a fine specimen of which,

¹ Numerous figures of the leaves of Mesozoic Cycadophyta will be found in Seward's *Catalogue of the Mesozoic Plants in the Department of Geology, British Museum*, Parts ii.-iv. 1895-1904. See also his *Fossil Plants*, vol. iii. chap. xxxix. 1917.

almost 4 feet high, with a girth of $3\frac{1}{2}$ feet, was found some years ago in the Isle of Portland, and is now set up in the Geological Department of the British Museum.¹ In favourable cases the Cycad-like stems are completely silicified, and their structure preserved with wonderful perfection. A number of important specimens of this nature, referred to many species, have been found in our own country, France, Italy, and other parts of Europe, but the United States of America are far richer than any other country in such material. No less than sixty species of silicified trunks of Cycadophyta have already been described from the Mesozoic of North America, ranging in age from the Upper Triassic to the Lower Cretaceous. In the Eastern States the Potomac beds of Maryland (approximately of Wealden age) have yielded nine species, but the richest localities are in the West, on the Rim of the Black Hills of Dakota and the Freezeout Hills of Wyoming; from the Upper Jurassic and Lower Cretaceous beds of these districts fifty or more species have been obtained. The specimens are very numerous; thus twenty-nine species from the Black Hills of South Dakota were represented by nearly 1000 more or less complete trunks.² The Cycadophyta of the American Mesozoic rival in palaeontological value the gigantic Saurian animals, with the remains of which they are often associated. Fig. 116 represents the trunk of *Cycadeoidea marylandica*, the first American fossil Cycad to be discovered; it was found about the year 1860, between Baltimore and Washington, by the geologist Philip Tyson. A species from Colorado was the first to be described; this was in 1876. Many years

¹ Seward, "On *Cycadeoidea gigantea*, a New Cycadean Stem from the Purbeck Beds of Portland," *Quarterly Journal of the Geol. Soc.*, vol. liii. 1897.

² See Wieland, *American Fossil Cycads*, Carnegie Institution, Washington, vol. i. 1906, and vol. ii. 1916, and the systematic works by Lester Ward, there cited.

elapsed before any further discoveries were made; it was not till 1893 that additional specimens came to light in Maryland and that the rich deposits of the Black Hills of Dakota began to be explored. In recent years



FIG. 116.—*Cycadeoidea marylandica*. The earliest discovered American fossil Cycad. From an original daguerreotype. Nearly thirty young fruits are marked in the present view by the groups of bract-scars interpolated between the old leaf-bases. About $\frac{1}{4}$ natural size. From Wieland.

Mexico has proved to be extraordinarily rich in fossil Cycads.

The vast majority of the Mesozoic Cycadophyta at present investigated differ essentially from the existing order Cycadaceae, and have been grouped under the

class Bennettitales or Cycadeoideae, which may be provisionally divided into the families Bennettiteae and Williamsonieae.

I. BENNETTITALES.—In a great number of cases, fructifications have been found in actual connection, or in close association, with the stems of Cycadophyta, and it is only in the rarest instances that these fructifications have proved to be of the Cycadean type, as known to us from its recent representatives. In an overwhelming majority of the fructifications belonging to the Mesozoic Cycadophyta (using that form of name, as suggested by Prof. Nathorst, to indicate a group enormously wider than our recent Cycadaceae), the structure of the organs of reproduction is found to have been totally different from anything known in the recent Order, and of a far more highly differentiated type. The main purpose of the present chapter is to give some account of these plants, which formed the dominant group of Cycadophyta in the Mesozoic period.

A. *Bennettiteae*

The first family to be considered is that of the Bennettiteae, so named from the type-genus *Bennettites*, founded by Carruthers in 1868, for several species, ranging from the Middle Oolite to the Lower Greensand. The characters of the genus were thus given by the author in his classic memoir: "*Trunk* ovoid, in transverse section elliptical, covered with the somewhat long permanent bases of the petioles. *Medulla* entirely cellular, with numerous gum-canals. *Wood* consisting of a thin interrupted cylinder of striated tissue, everywhere penetrated by medullary rays. *Fruits* borne on secondary axes, not protruding beyond the bases of the petioles." ¹

¹ Carruthers, "On Fossil Cycadean Stems from the Secondary Rocks of Britain," *Trans. Linnean Soc.* vol. xxvi. 1870.

The elliptical transverse section of the stem is not generally accepted as a generic or even a specific character, but on the whole the short description just quoted still holds good. The American palaeobotanists use Buckland's generic name *Cycadeoidea* in preference to *Bennettites*, and this usage has been adopted by Prof. Seward in his *Fossil Plants*.

The following account is based in the first instance on the observations of Carruthers (who laid the foundation of our knowledge of the group), Solms-Laubach, Lignier, and others, confirmed, as regards the fructification of *Bennettites Gibsonianus*, by a study of the original preparations. The still more important results obtained from the investigation of the American material by Dr. Wieland have profoundly modified our conception of the group, and will be considered in due course.

In external aspect the stems of the Bennettiteae presented the same general appearance as those of the recent Cycads in which the stem remains clothed in an armour of persistent leaf-bases (see Fig. 117, B). The dimensions were also of the same order. The stem of *B. Gibsonianus*, shown in Fig. 117, from Carruthers' paper, attained a maximum diameter of 11 inches; a considerable part of this diameter was made up of the persistent leaf-bases, as shown in the figure. The American species *Cycadeoidea marylandica*, represented in Fig. 116, was of larger dimensions, and may serve as a typical example of the external characters of the family. The great feature in which these stems differ, even in outward aspect, from those of any recent Cycads is the presence of numerous short lateral branches, resembling large buds, which are wedged in here and there between the bases of the leaves (Figs. 116, 117, *f*). These lateral appendages are the fructifications, one of which is shown in Fig. 117, A, in longitudinal section, inserted by a short stalk on the stem, and lying horizontally between the bases of the leaves. It is probable that the

position of the fructifications was axillary; in any case they were lateral branches, and cannot have been terminal on the main axis, thus differing in position from the cones

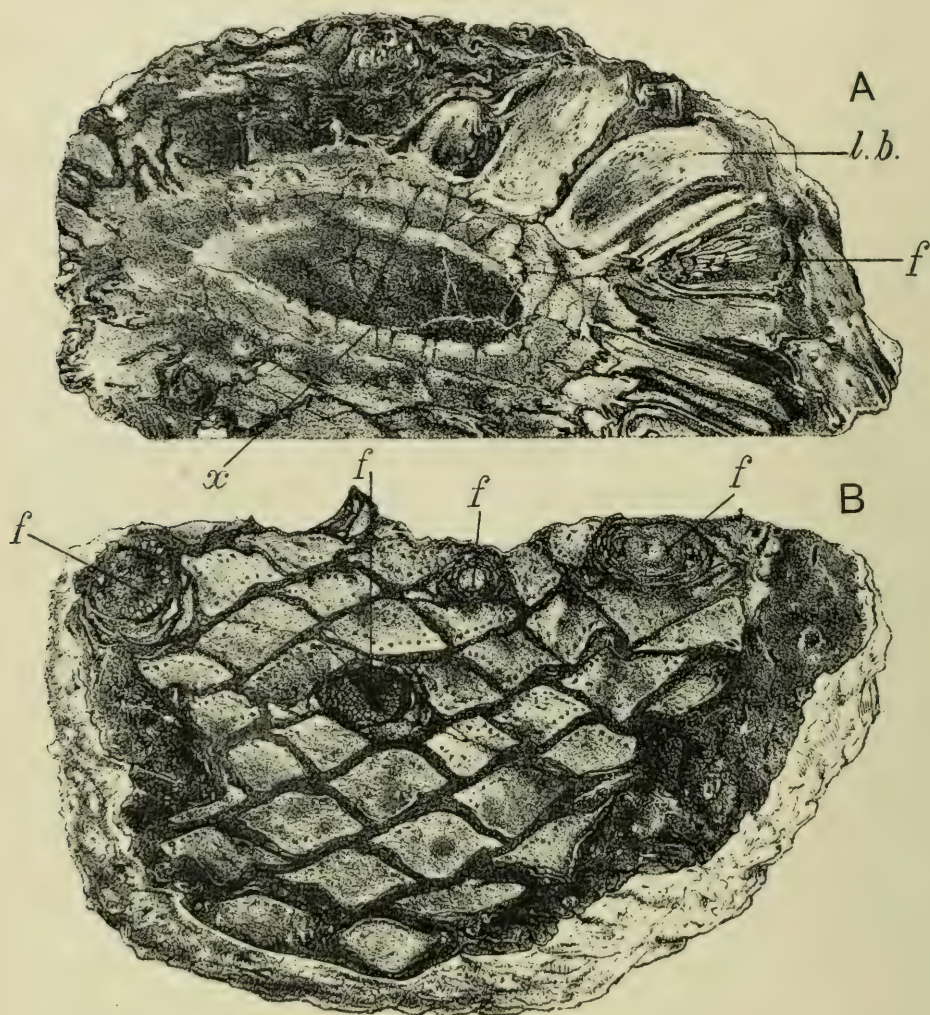


FIG. 117.—*Bennettites Gibsonianus*. A. Stem in transverse section, showing the ring of wood, *x*, surrounding the large pith, the leaf-bases, *l.b.*, completely covering the surface, and a fructification, *f*, seen in longitudinal section, between the leaf-bases. B. Stem in tangential section, through the armour of leaf-bases, the vascular bundles in which are shown. Several fructifications, *f*, are seen, in transverse section. Both reduced. From the *Linnean Soc. Trans.* After Carruthers.

of most living Cycads. Hence, the fertile stem of *Bennettites* appears to have had a monopodial, and not, as is usual in the recent Order, a sympodial construction.

The main features in the anatomy of the stem were

worked out by Carruthers, whose conclusions have been confirmed by the work of later investigators. The structure is shown with special clearness in *Bennettites Saxbyanus*, a species from the Wealden beds of Brook Point, in the Isle of Wight (see Fig. 118). The large pith is surrounded by a ring of wood and bast, of no great thickness, built up, as in normal Gymnospermous

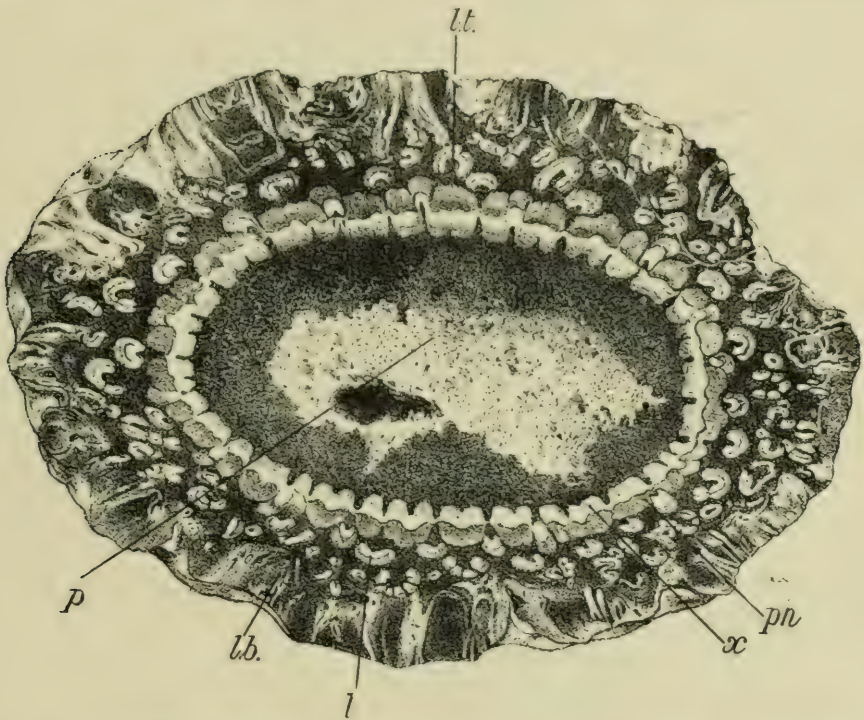


FIG. 118.—*Bennettites Saxbyanus*. Transverse section of stem. *p*, pith; *x*, wood, *ph.*, phloem, together constituting a ring of collateral bundles; *lt.*, leaf-trace bundles, passing out through the cortex, and subdividing repeatedly; *lb.*, bases of leaves, which clothe the stem. Reduced. From the *Linnean Soc. Trans.* After Carruthers.

stems, of anastomosing vascular bundles with collateral structure. The histological details of both wood and bast (which were minutely studied by Count Solms-Laubach in an Italian species, and more recently by Dr. Wieland in the American material) agree with the corresponding structures in some recent Cycads. The tracheides are usually scalariform, as in *Stangeria*.

It is only when we come to the course of the bundles

passing out to the leaves that important differences show themselves. In recent Cycads, as is well known to the botanical student, the course of the leaf-traces is peculiar and characteristic. To supply each leaf, two bundles leave the stele; they start near together, and, curving in opposite directions, pass nearly half way round the stem, thus entering the leaf-base on the opposite side from their starting-points. They then subdivide, to form the numerous bundles of the petiole. In their course through the cortex the outgoing bundles are connected by cross-branches with one another, as well as with other leaf-traces, and with the bundles of the primary ring.¹

In *Bennettites* the arrangement is a far simpler one. A single bundle leaves the ring, starting from the lower angle of one of the meshes, which (as shown in tangential section) are occupied by the primary medullary rays. As the leaf-trace passes out through the cortex, it assumes a horse-shoe form, with the concave side inwards. It then breaks up by successive subdivisions into a number of smaller bundles, which enter the base of the leaf (see Fig. 118, *l.t.*).

In the petiole the vascular bundles arrange themselves in an almost closed curve, slightly open and involuted towards the upper surface, as is well shown in tangential sections passing through the armour of leaf-bases (see Fig. 117, B).

In some Bennettiteae, as, for example, in the species *B. Peachianus*, from the Middle Oolite of Sutherland, the pith contains several isolated rings of differentiated tissue, which at first sight suggest medullary vascular strands, and were at one time erroneously compared with the central steles or "star-rings" of the Permian Medulloseae.² More recent observations leave no doubt

¹ See De Bary, *Comparative Anatomy of Phanerogams and Ferns*, English edition, p. 608.

² See above, Chapter III. p. 190. The statement, to this effect, in Solms-Laubach's *Fossil Botany*, p. 98, was corrected by him in his

that the medullary rings occurring in *Bennettites* have nothing to do with the vascular system, and consist merely of bands of internal periderm, an abnormal condition which is often met with in the stems of recent Cycads.

We see, then, that the structure of the Bennettiteae, so far as it is at present known, was a simple monostelic one, resembling in its main features that of the less complex Cycads now living, but differing from any existing Cycads in the simpler course of the bundles supplying the leaves. In this latter point, the Bennettitean stem was compared by Solms-Laubach with the peduncle of recent Cycads, an organ which in other points also appears to show a more primitive anatomy than that of the vegetative stem.¹

In *Cycadeoidea Yatesii*, and another English species, there is evidence for the presence of two or more successive zones of wood and bast, as in the recent *Cycas* and *Macrozamia*.

In *B. Gibsonianus* the vascular bundles of the leaf-bases are beautifully preserved, and show essentially the same structure as the foliar bundles of the recent Cycadaceae. They are of the collateral mesarch type, whereas those of the stem are endarch; the centripetal wood forms a mass of large elements, with a band of the radially arranged tracheae of the centrifugal wood on the outside. The same structure is found in various American species, but in *Cycadeoidea micromyela*, a French species probably of Liassic age, centripetal wood appears to be entirely absent.² The detailed structure of the xylem in the bundles of Bennettiteae still needs further investigation. Beyond the wood is the phloem,

joint work with Capellini, on the trunks of Italian Bennettiteae, *Mem. R. Accad. Sci. Bologna*, vol. ii. 1891.

¹ See Chapter I. p. 90.

² Lignier, "Végétaux foss. de Normandie, III. *Cycadeoidea micromyela*," *Mém. Soc. Linn. de Normandie*, t. xx. 1901.

often well preserved, and the outer edge of the bundle is occupied by a group of bast-fibres.

The parenchymatous tissue, both of the stem and leaf-bases, abounds in large gum-canals, the contents of which have often become fossilised. These organs closely resemble the similar secretory passages in recent Cycads.

Between the leaf-bases, and around the fructifications and their bracts, the spaces are densely packed with multicellular hairs, very different from anything known in Cycadaceae, but closely resembling the rammenta of Ferns. The hairs are scale-like structures, one cell thick near the margin, but reaching a thickness of from two to five cells in their middle part (see Fig. 120, B). The cells of which they are composed attain a great length in the longitudinal direction of the ramentum. The rammenta are borne both on the leaf-bases and on the bracts, which, as we shall see, envelop the fructification. The Fern-like character presented by the rammenta is a surprising homoplastic feature in a genus so far advanced in Phanerogamic organisation as *Bennettites*.

A stem, *Colymbetes Edwardsi*, Stopes, probably of Wealden age, shows an extraordinary structure. The large pith and the groups of primary wood are like those of other Cycadophytes; the peculiar feature is in the secondary wood, which consists of ten or more successive zones, all, as it appears, the product of a single cambium. The zones alternate, the elements of each zone running in a direction approximately at right angles to those of its neighbours, vertically in the one, horizontally and tangentially in the next, and so on. This has the curious effect that the transverse and radial sections appear just alike, every alternate zone being cut radially in transverse section and transversely in radial section and *vice versa*. All the zones, however, are quite continuous one with

another. This remarkable structure appears to be without analogy.¹

Dr. Marie C. Stopes has also described, under the name *Bennettites Scottii*, the smallest known Bennettitean stem; the specimen (of unrecorded locality and horizon) measures 8.5 cm. in total height and 7×5 cm. in diameter. Well-preserved young fronds are attached to the axis, the whole having a bud-like character. All the anatomical features of the genus are shown. In the vascular bundles of the leaves the whole of the xylem is centripetal, perhaps on account of their youth. The ramenta (unlike those of *B. Gibsonianus*) are only one cell thick. A dense covering of hairs, distinct from the ramenta, clothes the under-side of the pinnae. There are indications of an abscission-layer at the base of the specimen, suggesting that it may have been a lateral bud, detached from a larger stem.²

The same author has further described, for the first time, roots or rootlets attributable to a *Bennettites*, probably *B. Saxbyanus*. The roots, about 1 mm. in diameter, are traversed by a strand of scalariform tracheides, and are clothed with long and numerous root-hairs.³

We now come to the consideration of the fructifications themselves, and in approaching this subject we must divest our minds of all preconceptions drawn from a knowledge of existing Cycadean cones. The reproductive organs of the Bennettitales are wholly different in organisation, both from the cones which characterise

¹ See M. C. Stopes, *Catalogue of the Cretaceous Flora*, Part ii, p. 314, British Museum, 1915. For *Cycadeoidea Yatesii*, referred to above, see p. 295 of the same volume.

² M. C. Stopes, "*Bennettites Scottii*, sp. nov., a European Petrification with Foliage," *Journal of Linnean Society, Botany*, vol. xlv. 1920, p. 483.

³ M. C. Stopes, "Roots in *Bennettites*," *Ann. of Bot.*, vol. xxxi. 1917, p. 257.

the majority of recent Cycadaceae, and from the rosette of leaf-like carpels which forms the female system in the genus *Cycas*.

The following description of the fructification is based, in the first instance, on the species *Bennettites Gibsonianus*¹ of Carruthers. In this species only the female organs are known, but, as we shall see later, the investigation of the American material has proved that in most cases, and possibly in all, the fructification was hermaphrodite. We have already learnt that each fructification is a lateral appendage, seated by a short stalk on the main stem. The whole fruit is somewhat pear-shaped, and about 5 cm. in extreme length. Although fully ripe in the specimens investigated, as shown by the condition of the seeds, the fruit is completely enclosed in imbricated bracts, which spring from the stalk, and close in over the apex (see diagram, Fig. 120, A, and Fig. 119).

The stalk is expanded into a hemispherical receptacle, on which all the organs of the fruit are inserted. From the convex surface of the receptacle spring a great number of slender pedicels, which pass vertically upwards, or diverge slightly towards the curved surface of the fruit. Each of these pedicels bears at its end a single erect seed, with the micropyle directed outwards (see Fig. 119, and diagram, Fig. 120, A). The seeds are so placed that their micropyles meet the surface of the fruit approximately at a right angle.

The spaces between the pedicels are packed with sterile appendages, which may be called the interseminal scales. Towards the periphery of the fruit, in its lower portion, the sterile organs are more numerous than else-

¹ The original specimen of this magnificent fossil was found by Mr. T. F. Gibson in 1856 or 1857 in the Lower Greensand at Luccombe Chine, in the Isle of Wight. Part of the specimen is now at Kew, and part at the British Museum (Natural History). A second specimen was afterwards discovered by Dr. Leeson, of Bonchurch, Isle of Wight.

where, and around the base of the receptacle the former are present alone (Fig. 120, A).

All the organs of the fruit are closely packed together, and at its periphery (*i.e.* immediately within the enveloping bracts) the tissue appears to be actually continuous, forming, as it were, a closed pericarp, perforated only by the micropyles of the seeds (see Fig. 120, A and D, *p*). The pericarp is formed by the cohesion of the interseminal scales. These organs are dilated at their distal ends, between the seeds, so as to form a continuous envelope, only interrupted by narrow pits, into which the seeds exactly fit (see Figs. 119 and 120, A, and *cf.* Fig. 123). In the lower part of the fruit, below the region of the seeds, the pericarp is formed by the union of the outer and shorter scales. In order to make the somewhat complicated arrangement more intelligible, we may further quote Count Solms-Laubach's summary: "We have in the fructification (spadix) two kinds of organs of different character and closely crowded to-

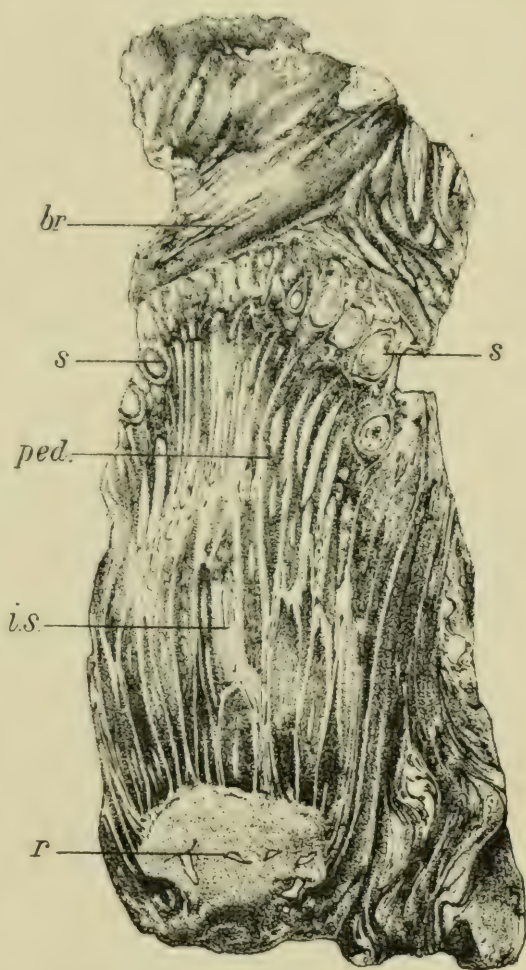


FIG. 119. — *Bennettites Gibsonianus*. Longitudinal section of a fructification. *r*, receptacle; *br*, bracts, enclosing the fruit; *s*, seeds, each borne at the summit of a long pedicel, *ped.*; *i.s.*, interseminal scales. \times about 2. From *Linnean Soc. Trans.* After Carruthers.

gether: the seed-stalks (cords) [our pedicels] diverging

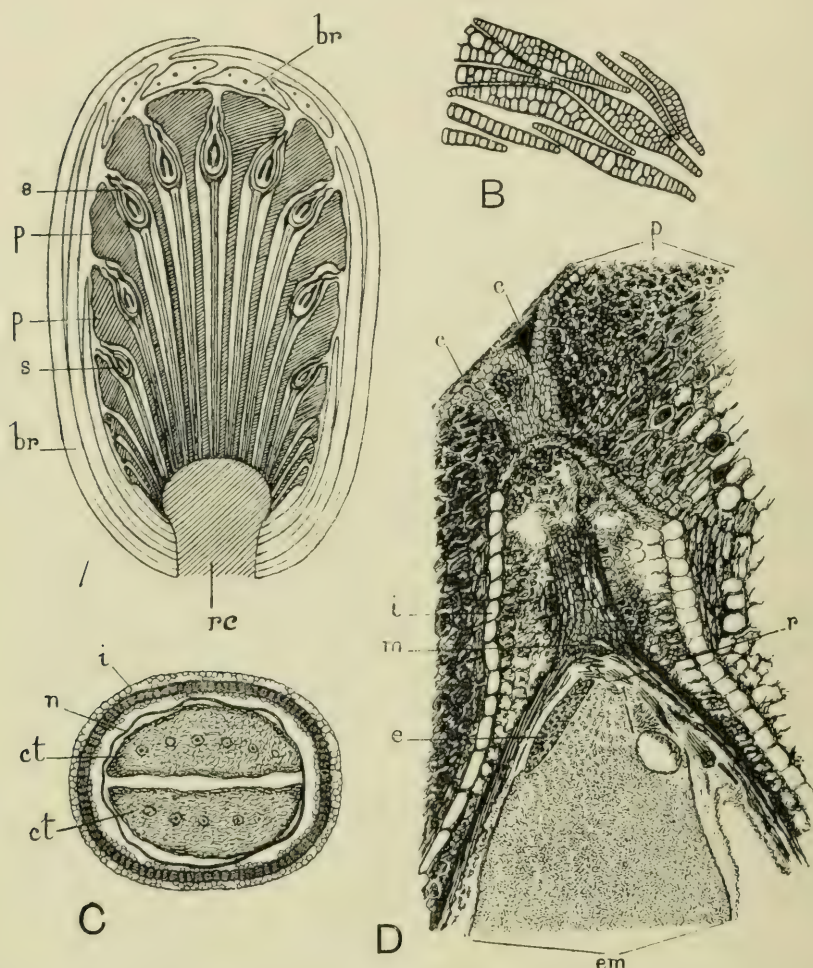


FIG. 120.—*Bennettites Gibsonianus*. A. Diagram of the fruit, in radial section. *rc*, receptacle; *br*, bracts, which overlap at the top of the fruit; *s*, seeds, each borne on a long pedicel, springing from the receptacle; in each seed the dicotyledonous embryo is indicated; *p*, dilated ends of the interseminal scales, which, in nature, are more numerous and become confluent, forming the pericarp. Modified, after Solms-Laubach and Potonié. B. Ramanta, in transverse section. \times about 15. C. Transverse section of a seed. \times about 12. S. Coll. 350. D. Somewhat oblique longitudinal section through the micropyle of a seed. *em*, radicular end of embryo; *r*, apex of radicle; *e*, remains of endosperm (?); *m*, micropyle, obliquely cut by the plane of section; *i*, outer layer of testa; *p*, part of pericarp; *c*, *c*, crevices in pericarp, corresponding to the limits of its constituent interseminal scales. \times 20. S. Coll. 357. The original figures B, C, and D, as well as Figs. 121 and 122, are from sections cut for Count Solms from the type-specimen, and now in the Scott collection. (G. T. G.)

above, cluster-wise, and each terminating in a seed; and the interstitial organs [our interseminal scales],

increasing constantly in length from the periphery of the cluster towards the inside, appearing by themselves in the periphery, but mixed with the seed-stalks further in, overtopping the seeds with their apices, and forming by the union of their apices the homogeneous tissue-layer of the surface of the fructification. In consequence of this arrangement, every seed is sunk in a pit, the orifice of which then narrows over the seed, owing to the lateral outgrowth of its walls.”¹

This description should be compared with the diagram, Fig. 120, A, and with the more detailed Figs. 119, 120, D, and 121. We will now take the various constituent organs of the fruit, and consider their structure a little more in detail.

The receptacle forms, as we have seen, the enlarged termination of the axis of the fruit. The peduncle has a structure like that of the stem, on a small scale, and the bundles given off to the bracts divide up like those of the vegetative leaves, though only to a small extent. A remarkable feature in the anatomy of the peduncle is the great development of the phloem, which much exceeds the wood in thickness. This peculiarity, which recurs in some of the American species, may be explained by the great demands on the organic food-supply made by the crowded reproductive organs, and especially by the seeds. In the vegetative stem, however, the phloem is also largely developed. The receptacle itself is poorly preserved, but shows here and there sections of collateral vascular bundles, on their way out to the appendages.

The bracts have, on the whole, the structure of reduced foliage-leaves. Their outer surface is clothed by ramenta, and stomata have been detected in their epidermis.² Towards the inner surface of the bract, the mesophyll has a fibrous structure, but the bulk of the parenchyma

¹ “On the Fructification of *Bennettites Gibsonianus*,” *Annals of Botany*, vol. v. 1891, p. 446.

² C. A. Barber, in MS.

is formed of short cells with a curious scalariform thickening on their walls. Several large gum-canals traverse the bract, which in this species usually contains three vascular bundles. These bundles are reduced in structure, but near the base, where they are best developed, they seem to be of the mesarch type usual in the foliar bundles of Cycads.

The seed-pedicels, which are seen in great numbers in the transverse section of the fruit (see Fig. 121), have



FIG. 121.—*Bennettites Gibsonianus*. Transverse section of fruit, not quite complete. *b*, bracts; *s*, seeds, ranged in a ring around the fructification; *p*, pedicels, belonging to other seeds, borne at a higher level; between the pedicels the interseminal scales can be recognised. The pericarp is the dark zone in which the seeds are embedded. \times about 3. From a photograph by Dr. Bousfield. S. Coll. 350.

an approximately cylindrical form, with their sides somewhat flattened by pressure. Through the middle of each pedicel runs a vascular bundle, which, so far as the preservation allows of an opinion, appears to have had a concentric structure. Outside the vascular strand is a well-marked bundle-sheath, succeeded by a wide cortex ¹

¹ It has been suggested, however, that the "bundle-sheath" is really the boundary of the cortex, and that the wide surrounding zone is wholly made up of a many-layered epidermis. Cf. p. 338.

and an epidermis of tubular cells. The whole is surrounded by the epidermis belonging to the adjacent interseminal scales.

Each pedicel terminates directly in an orthotropous seed. The xylem of the bundle ends at the chalaza in a small disc or cup of tracheides, while the adjacent tissues of the pedicel pass over into the testa. The seeds have a length of over 3 mm., not counting the micropylar tube, and a diameter of nearly 2 mm. The seeds which have been investigated were fully ripe, for each, when well preserved, contains a large embryo, nearly filling the cavity (see Figs. 121, *s*, 120, *C*, and 122). The testa is made up of three layers, an inner and outer layer of small comparatively thin-walled cells, and a middle layer of large square or palisade-like cells, which appear almost solid, an appearance which may be due to extreme thickening of their cell-walls (Fig. 120, *C* and *D*).

Towards the micropyle, the middle layer of the testa is greatly dilated, and is here several cells in thickness; it is surrounded by the external zone, which in this part is very distinct (Fig. 120, *D*). The inner layer of the testa forms the internal tube of the actual micropyle, which, however, in these ripe seeds is closed, as is usually the case (see Fig. 120, *D*, which represents a somewhat oblique longitudinal section through the micropylar end of a seed). The distal end of the micropyle (not shown in our figure) narrows out considerably, owing to reduction of the middle layer of cells, but appears to be somewhat dilated again at the extremity. The testa is everywhere closely adherent to the surrounding tissue of the pericarp. In the body of the seed, the nucellus is only to be traced as a structureless membrane (see Fig. 120, *C*, *n*), but it is better preserved at the apex (Fig. 120, *D*, *m*).

The embryo so nearly fills the cavity of the seed that the latter may be spoken of as exalbuminous, though it is quite possible that here, as in most so-called exalbuminous seeds, some slight remains of the endo-

sperm persisted. The small mass of tissue marked *c* in Fig. 120, D, in which the nuclei appear to be preserved, may probably be a portion of the remaining endosperm,¹ though it might also be interpreted as belonging to the root-cap of the embryonic radicle.

The embryo is very well preserved, indeed the Bennettiteae afford the only cases in which it has been possible to study the embryos of fossil plants in detail. The embryo is a typical dicotyledonous one, with the pointed

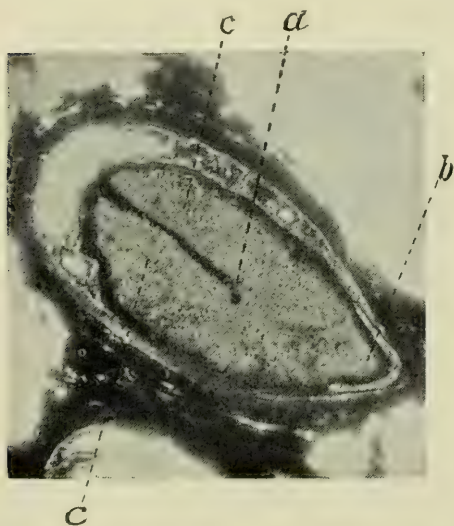


FIG. 122. — *Bennettites Gibsonianus*. Longitudinal section of seed, showing dicotyledonous embryo. *c, c*, the two cotyledons; *a*, apex of plumule; *b*, radicle. $\times 12$. From a photograph by Dr. Bousfield. S. Coll. 351.

radicle directed towards the micropyle. The hypocotyl is short; more than half the whole length of the embryo is occupied by the two thick cotyledons, the surfaces of which are in contact (see Figs. 120, C, 122). Between them the growing point of the plumule has been recognised in favourable preparations (Fig. 122, *a*). The tissue of the embryo is to some extent preserved, and the position of the young vascular bundles in the cotyledons

can be determined (see Fig. 120, C, which represents a seed in transverse section, passing through the two cotyledons (*ct*). The vascular cylinder of the hypocotyl has also been recognised, and its connection with the cotyledonary bundles traced.² The number of seeds in which the embryo is well preserved, both in this fossil and in other species, is so considerable as to leave no doubt regarding

¹ On the possible presence of endosperm see also Wieland, *American Fossil Cycads*, vol. ii. 1916, p. 141 (*Cycadeoidea Wielandi*).

² Solms-Laubach, *l.c.* p. 440.

the correct interpretation of the main facts. The general structure of the dicotyledonous embryo is in no way surprising in a plant of Cycadean affinities, but the practically exalbuminous character of the seed is without example among recent Gymnosperms. Of course, in speaking of Bennettiteae as Gymnosperms, we are referring rather to their presumed affinities than to the actual structure of the fruit, which comes very near to being angiospermous.

The interseminal scales, which combine to form the pericarp, have proved difficult to investigate, owing to their state of preservation. In their lower part, where they pass between the pedicels of the seeds, they are crushed out of shape, and much disorganised, so as to be reduced in many cases to a vascular bundle with an irregular epidermis loosely surrounding it, the intermediate tissue having disappeared. The interseminal scales are somewhat similar in structure to the pedicels of the seeds, but the homologies of their respective tissues are not yet clearly understood.

The expanded outer ends of the interseminal scales unite to form the "pericarp," a dense, apparently continuous zone, starting at the base of the fruit, from the sides of the receptacle, and extending, with increased thickness, over the top. In its upper portion, as already explained, it encloses the seeds, and is perforated by their micropyles. Its external surface is furrowed, the furrows forming a network. The pericarp, from its dense structure, has at first sight the appearance of a distinct organ of the fruit, but, as above stated, there is no doubt that it is in reality built up of the distal parts of the interseminal scales (Fig. 120, A). The furrows thus correspond to the lines of junction of the constituent scales. The outer surface is coated by a distinct epidermis, which extends into and lines the furrows (see Fig. 120, D, *c*; cf. Fig. 123). The inner tissue of the pericarp-zone (*p*) is formed of parenchymatous cells, with moderately

thick walls and abundant dark contents, perhaps indicating the presence of some reserve food-substance during life. Tangential sections of the upper part of the fruit show the micropyles of the seeds, lying at the angles where the limits of the constituent interseminal organs meet. In Fig. 120, D (from a radial section),

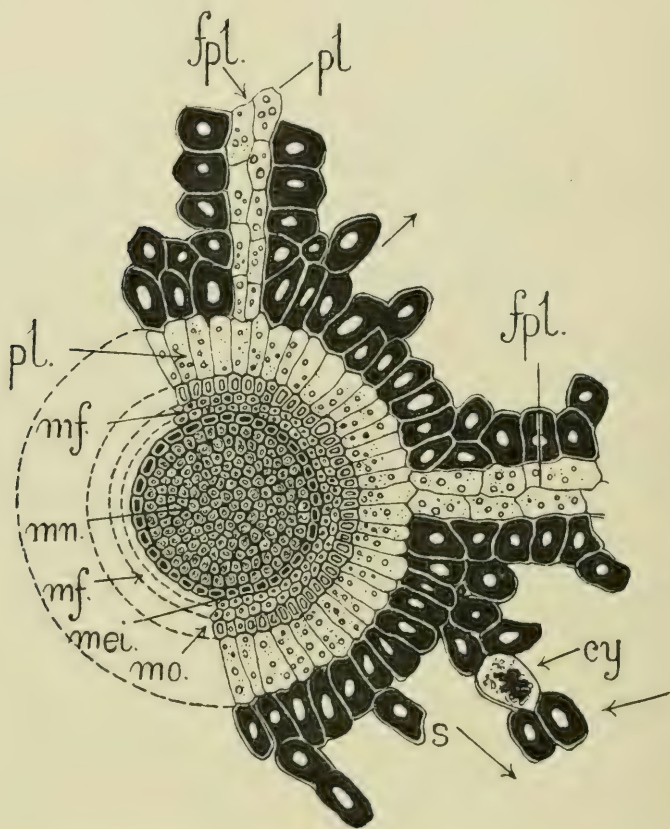


FIG. 123.—*Bennettites albianus*. Transverse section through micropyle of a seed and parts of surrounding interseminal scales. *mn*, nucellar mass plugging micropyle; *mei*, inner limiting layer of micropyle tube; *mf*, fibrous layer; *mo*, outer layer of micropyle; *pl*, epidermal layer of scales, adhering to micropylar tube; *fpl*, similar layers of scales, fused; *s*, stone-cells of scales; *cy*, a crystal-cell. \times about 80 (?). After M. C. Stopes.

two of the furrows marking these limits (*c*) are shown close together, having been cut at a short distance from the micropyle towards which they converged. Vascular bundles run out into the pericarp between the seeds, and are the continuation of those seen in the lower portion of the interseminal scales.

So far as the bracts and gynaecium are concerned, the classic *Bennettites Gibsonianus* may still serve as a type of the complex Bennettitean fructification. Other similar European examples have been described, among which one from Normandy, called *Bennettites Morierei*, and probably derived from the Gault, was fully investigated by Prof. Lignier of Caen.¹ The specimen is a detached fruit, not known in connection with the stem on which it grew. It has hence been supposed that it may have had a longer stalk than that of *B. Gibsonianus*, and so may have been more easily detached. The fruit is somewhat larger than in our English species, with which, however, it agrees in all essential points of structure. The exceptionally beautiful preservation enabled Prof. Lignier to work out the details of structure with remarkable precision.

A remarkable Bennettitean fruit from the Gault of Folkestone has recently been described by Dr. Marie C. Stopes under the name *Bennettites albianus*.² Though only a fragment, 55×30 mm. in area, the specimen is exceptionally well preserved. The fruit, when complete, must have been much the largest known in the family; it could not have been less than 70 mm. in diameter, and the curvature of the surface in the portion preserved suggests a diameter of as much as 120 mm. The diameter of the fruit of *B. Morierei*, one of the largest previously known, is little more than 30 mm. The number of seeds was likewise enormous; a single transverse section of the fragment contained 250, and it is estimated that the total number in the complete fruit may have run into thousands. It is probable that the form of the whole was flatter and more cushion-like than in other Bennettiteae.

¹ O. Lignier, *Végétaux fossiles de Normandie*, "Structure et affinités du *Bennettites Morierei*," Caen, 1894. "Le *Bennettites Morierei*, ne serait-il pas d'origine infracrétacée?" *Bull. de la Soc. Linn. de Normandie*, sér. 6, vol. ii. 1909.

² M. C. Stopes, "New Bennettitean Cones from the British Cretaceous," *Phil. Trans. Royal Soc.*, Series B. vol. 208, 1918, p. 389.

The general construction of the fruit is on the same lines as in other species, but the terminal expansions of the interseminal scales are more completely fused and are composed of highly sclerotic tissue, forming a strong and hard pericarp. In the completely fused region the epidermis is lost, but it reappears higher up in the form of the very distinct "plastid-layer," which is united to the micropylar tubes of the seeds as well as to the adjacent scales (Figs. 123 and 124, B).

The vascular strands, both of the interseminal scales and of the seed-pedicels, are little developed. In the latter the wide apparent "cortex" is regarded by the author as representing a many-layered and lacunar epidermis of tubular cells, possibly forming a spongy water-holding tissue, compensating for the scanty vascular supply. The base of the seed is embedded in an aril-like cup, formed by the tubular cells; they are reduced to a single layer above, where they constitute a kind of cupule round the seed (Fig. 124, A).

The seeds are small and slender, not more than 1.2 mm. in diameter; the apex usually has five ribs. Inside the cupule there is a "deliquescent layer" of a transitory nature, while the integument proper consists of three layers, the outer stony and square-celled, the middle stony and fibrous, and the inner thin-walled. The same layers can be recognised, in a modified form, in the micropylar region (Fig. 123). The vascular supply is provided by a single, very small strand, which dies out in the base of the nucellus (Fig. 124, B). The micropyle is plugged by an outgrowth from the nucellus; a cavity in the plug probably represents the pollen-chamber (Fig. 124, B). The seeds appear to be without endosperm; the usual dicotyledonous embryo is present, but the hypocotyl and radicle are relatively more massive than in other species.

As Dr. Stopes points out, there is no evidence for the presence of two integuments in the Bennettitean seed.

Neither does the plugging of the micropyles in the ripe fruit afford any presumption of parthenogenesis, as

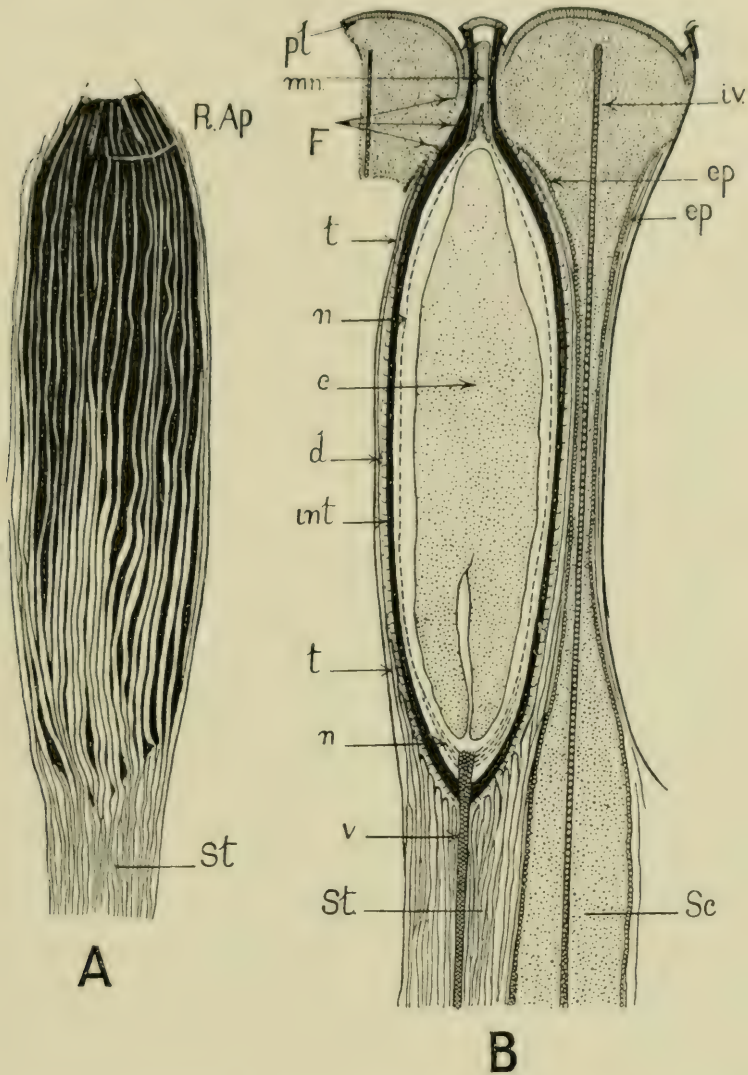


FIG. 124.—*Bennettites albianus*. A. Restoration of seed, enclosed in its "cupule" of tubular cells (not all shown) extending from the seed-stalk. *R.Ap.*, ribbed apex; *st*, stalk. B. Restoration of seed and adjacent scales in median longitudinal section. *int*, integument of seed; *d*, "deliquescent layer"; *t*, tubular cells of "cupule"; *n*, nucellus; *mn*, nucellar plug in micropyle; *e*, embryo; *st*, seed-stalk; *v*, its vascular bundle, dying out in base of nucellus; *F*, region of fusion of intersemental scales with micropyle of seed; *sc*, intersemental scale; *iv*, vascular strand of scale; *ep*, lateral epidermis of scale; *pl*, upper epidermis, running also round micropyle-neck. After M. C. Stopes.

Lignier supposed. The micropyle may well have been open at the pollination stage.

The hard and massive fruit of *B. albianus* represents the culminating point of differentiation in this respect, among the known Bennettiteae. The Gault is a late horizon for the family, which may then have reached its extreme development, as it approached extinction.

It is, however, to the investigation of the magnificent American material that the remarkable progress during the present century in our knowledge of Mesozoic Cycadophyta is principally due, and some account of the chief results attained must now be attempted.

As regards habit, the American, like the contemporary European Bennettiteae, seem to have been plants of no great stature; there is no evidence at present for trunks of a height of more than 10 or 12 feet, while the great majority of the stems were quite short, like that shown in Fig. 116. In some cases the stems were nearly spherical; often several are connected together as branches of the same stock. In seeking analogies among recent Cycads we must therefore go to the shorter-stemmed genera, such as *Bowenia* or *Stangeria*, or certain *Macrozamia*s, rather than to tall plants like *Microcycas* and various species of *Cycas* and *Dioon*.

So far as the foliage and the external features of the trunk are concerned, the remarks made at the beginning of the chapter apply to the American as well as to the European forms. The latter are now included by their investigators in Buckland's genus *Cycadeoidea* (synonymous with *Bennettites* of Carruthers¹); a new genus, *Cycadella*, founded by Lester Ward for a number

¹ The name *Cycadeoidea* has been employed by some European writers for trunks of the Bennettitean type without fructifications, as in the case of Prof. Seward's *Cycadeoidea ingens*. In discussing the American species I follow the usage of the palaeobotanists of that continent, employing the name *Cycadeoidea* throughout. Prof. Seward has recently adopted the name *Cycadeoidea* in preference to *Bennettites* for the whole group. See his *Fossil Plants*, vol. iii. p. 370. This is the consistent course, but, in agreement with Dr. Wieland's practice, the familiar name *Bennettites* is here kept up for the European species.

of dwarf stems, from the Jurassic of Wyoming, distinguished by their abundant ramental covering, has since been merged in *Cycadeoidea* by Dr. Wieland.

Anatomically, the American stems so far investigated agree wonderfully closely, often down to the most minute detail, with the European species of *Bennettites*. It is, however, quite probable that when the investigation of the vast material has proceeded further, more variety may be found. As regards the form and structure of the leaves of the Bennettiteae, our first information came from Dr. Wieland, who in various specimens succeeded in finding the young leaves still folded in the bud and preserved in great perfection. His observations were originally made on *Cycadeoidea ingens*, a species in which he estimates the length of the mature leaf at about 10 feet, and on *C. (Cycadella) ramentosa*, a much smaller plant, so that both the later and the earlier types are represented. It is sufficient, without going into details, to say that Dr. Wieland's investigations show that in form, pefoliation, venation, and anatomical structure these leaves show a close agreement with those of recent Cycads of the suborder Zamieae; the vascular bundles were collateral and mesarch, without radial arrangement of the centrifugal wood or phloem. Speaking especially of *Cycadeoidea ingens*, Dr. Wieland says: "Were one to adjudge the taxonomic position of the fossil species on the basis of its foliage only, one might, bearing in mind the general absence of scale-leaves, place it near *Macrozamia* or *Encephalartos*."¹ The leaves of *C. ramentosa* only differ in details; the structure of the pinnules is found to be almost identical with that in the recent *Bowenia*.² This close correspondence in foliar characters with the recent Cycadaceae is the more remarkable when we consider how totally the two groups differed in their reproductive organs, the organisation of which was first fully revealed by Dr. Wieland's researches.

¹ *American Fossil Cycads*, vol. i. p. 94.

² *L.c.* p. 101.

The European specimens had yielded scarcely any information as to the nature of the microsporangiate organs of the Bennettiteae. In an Italian species, *Cycadeoidea etrusca*,¹ bodies interpreted as pollen-grains were discovered by Count Solms-Laubach in the interior of a fructification, lying in the space between the apex of the ovuliferous receptacle and the surrounding bracts. Though, owing to bad preservation, the stamens were not detected, the inference was drawn that they were probably borne in the same fructification with the ovules. This suggestion has been completely confirmed by the investigation of the perfectly preserved specimens which have since come to light in America.

The male sporophylls of the Bennettiteae were first discovered in 1899, in the Dakota species *Cycadeoidea ingens*, already referred to ;² their relation to the gynaecium was established two years later, in the same species, when the organisation of the hermaphrodite or bisexual flower was described for the first time.³ Numerous trunks with bisexual fructifications, belonging to various American species, have now been investigated. The fructifications were borne laterally on the stem, precisely in the same way as those of *Bennettites Gibsonianus* and other European forms, which were probably also bisexual (see p. 321). The plant bore a considerable number of fructifications at the same time (see Fig. 116) ; on a single specimen of *Cycadeoidea dacotensis* sixty-one fruits, all more or less at the same stage of

¹ The specimen was found on an Etruscan tomb at Marzabotto near Bologna ; Capellini and Solms-Laubach, " I tronchi di Bennettitee dei Musei Italiani," *Mem. d. R. Accad. delle Sc. dell' Ist. di Bologna*, series v. vol. ii. 1892. Dr. Wieland, who reinvestigated the fructifications and found some further remains of structure, compares them with those of the *Cycadella* species. See his " Historic Fossil Cycads," *Amer. Journal of Science*, vol. xxv. February 1908, p. 93.

² Wieland, " A Study of some American Fossil Cycads, Part i. The Male Flower of *Cycadeoidea*," *Amer. Journ. Science*, vii. 1899.

³ *L.c.* Part iv. " On the Microsporangiate Fructification of *Cycadeoidea*," *Amer. Journ. Science*, xi. 1901.

development, were counted, and Dr. Wieland is inclined to think that the plants were "monocarpic," fruiting once for all and then perishing, as is the case with many Palms and Bamboos at the present day. This opinion has been much strengthened by his later work, to which we shall refer.

The structure of the bisexual fructification or "flower," as it may be appropriately called, will first be described in the case of *Cycadeoidea dacotensis*, one of the species most fully investigated. It may, however, be said at once that few important differences in the floral morphology of the different species have been detected. Some recent observations will be mentioned below.

The whole fructification has a length of about 12 cm., protruding somewhat beyond the leaf-bases of the trunk. (See the restored section shown in Fig. 125.) About half this length consists of the stout peduncle, which bears 100 or more spirally arranged bracts on its upper part. The centre of the flower is occupied by the ovu-

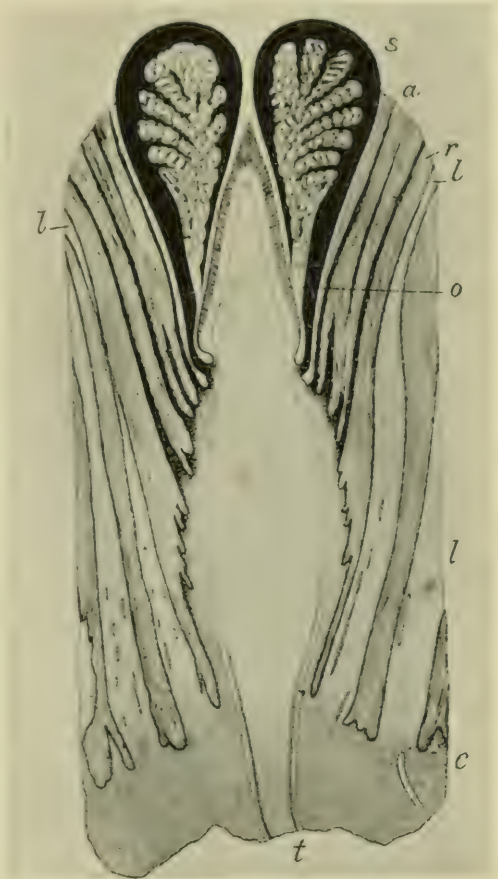


FIG. 125.—*Cycadeoidea dacotensis*. Median longitudinal section of a bisexual flower. The peduncle, with the surrounding leaf-bases and bracts, is drawn from one section; the ovulate cone and microsporophylls are drawn from several other sections of similar strobili. *s*, the incurved microsporophylls; *o*, the ovuliferous cone; *a*, eroded outer border of the armour and bracts, forming the trunk-surface; *r*, ramenta between outermost bracts and adjacent leaf-base; *l*, leaf-base; *c*, cortex of trunk; *t*, bundles supplying peduncle. About $\frac{2}{3}$ natural size. From Wieland.

liferous receptacle, about 4 cm. in height, terminating the peduncle, as in *Bennettites Gibsonianus* (cf. Fig. 120, A). In *C. dacotensis*, however, the form of the receptacle is much more acutely conical, and the stage of development, in the present case, is a far earlier one, minute



FIG. 126.—*Cycadeoidea dacotensis*. Longitudinal section through the summit of an unexpanded bisexual flower. In the middle is the upper part of the ovuliferous cone, showing the zone of ovules and interseminal scales and the terminal tuft. To the right and left the compound stamens are seen, with their tips unfolded parallel to the sides of the central cone. The upper curved portion of each stamen is missing (cf. Fig 125, s). The pinnae, each bearing a series of synangia, are cut longitudinally. On the outside of all are the bracts. $\times 2$. From a photograph. After Wieland.

immature ovules taking the place of the ripe seeds of the specimens previously described.

The stalked ovules and interseminal scales here form a layer only 1.5 mm. in height (see Fig. 126, where this zone is better shown), whereas in the mature, seed-bearing condition these organs have grown to at least ten times the length. We have, in fact, at the stage now under consideration, to do with a *flower*, while the

fructification, described above, in *Bennettites Gibsonianus* and other species, was already a *fruit*. The receptacle bears ovules in its middle region; the base and apex are sterile, and clothed only with the barren interseminal scales, which at the apex are prolonged into a tuft (Fig. 126). The details of structure of the ovules at this stage have not yet been made clear.

Surrounding the ovuliferous cone, and enclosed by the bracts, is the whorl of compound microsporophylls which forms the most striking feature of the flower. The microsporophylls, or stamens, are numerous, numbering from eighteen to twenty in *C. dacotensis*, and are ranged in a single verticil; they are inserted hypogynously, below the base of the gynaecium (see Fig. 125), and their stalks are united to form a continuous sheath (the "disk" of Wieland), like the monadelphous stamens of a Mallow (see diagrams, Figs. 127 and 128). The connate sheath extends up to about the height of the top of the gynaecium; at this level the stamens become free from each other; they are large and complex structures about 10 cm. in length, if straightened out; they are always found, however, to be infolded in a circinate manner, the sporophylls curving over towards the gynaecium, so that their deflexed tips reach down almost to its base (see Figs. 125 and 126). Each stamen is a pinnately compound leaf with about twenty pairs of alternate pinnae, directed inwards from the concave side of the whole organ (Figs. 125 and 126; cf. the diagrams, Figs. 127 and 128). The apical and basal pinnae are sterile; all the rest bear synangia, arranged in two rows, the synangia numbering about ten in each row in the case of the longest pinnae. If, with Dr. Wieland, we regard each synangium as representing a reduced pinnule, the whole sporophyll must be called bipinnate. The stamen was thus a highly complex organ, recalling the fertile frond of a Fern rather than the comparatively simple type of microsporophyll which we meet with in the stamens of the higher plants.

The elaborate organisation of the whole flower is well shown in the diagrammatic figures 127 and 128, drawn by Dr. Wieland to represent the flower in an expanded condition. These diagrams are based on the species *Cycadeoidea ingens*, in which the number of stamens is less than in *C. dacotensis*. It will be noticed that the arrangement of the parts is just the same as in a typical

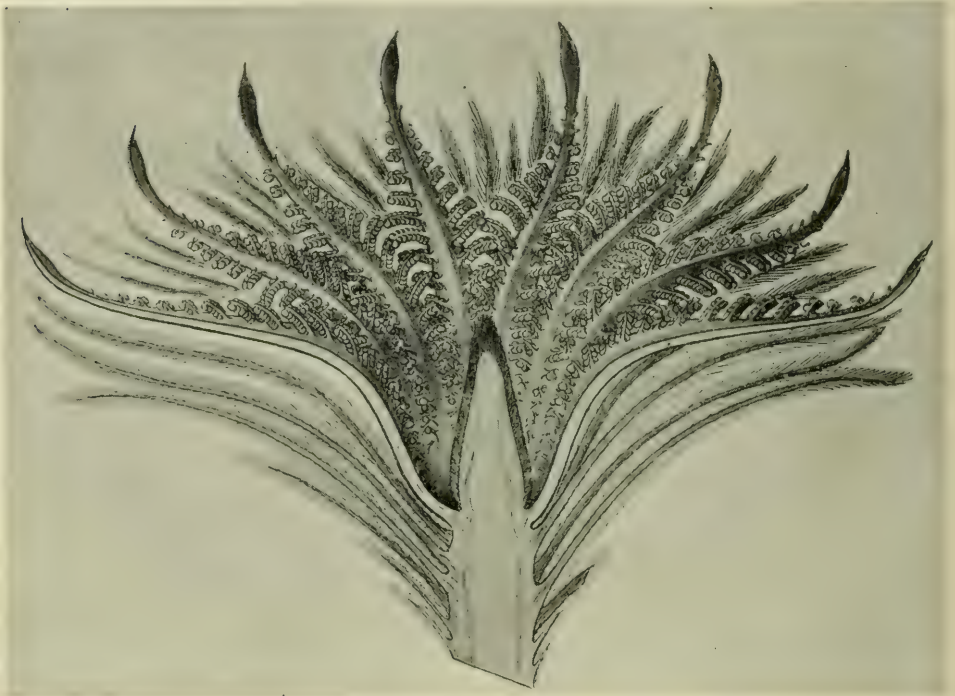


FIG. 127.—*Cycadeoidea ingens*. Restoration of an expanded bisexual flower in longitudinal section, showing the central ovuliferous cone, the hypogynous whorl of pinnately compound stamens, bearing numerous synangia, and the surrounding bracts, hairy with ramenta. About half natural size. From Wieland.

Angiospermous flower, with a central superior gynaeceum, a whorl of hypogynous stamens, and an enveloping perianth, here represented by the bracts.

The anatomical structure of the microsporophylls has not yet been fully investigated, but it is known that two ranks of vascular bundles are present in the connate disk, and that a considerable number enter each rachis as it becomes free. The general arrangement of

the bundles is compared with that in the rachis of a Cycad leaf.

The synangia, as already mentioned, are inserted in two rows on each pinna; their insertion is described by Dr. Wieland as "sub-lateral." Such a position is common

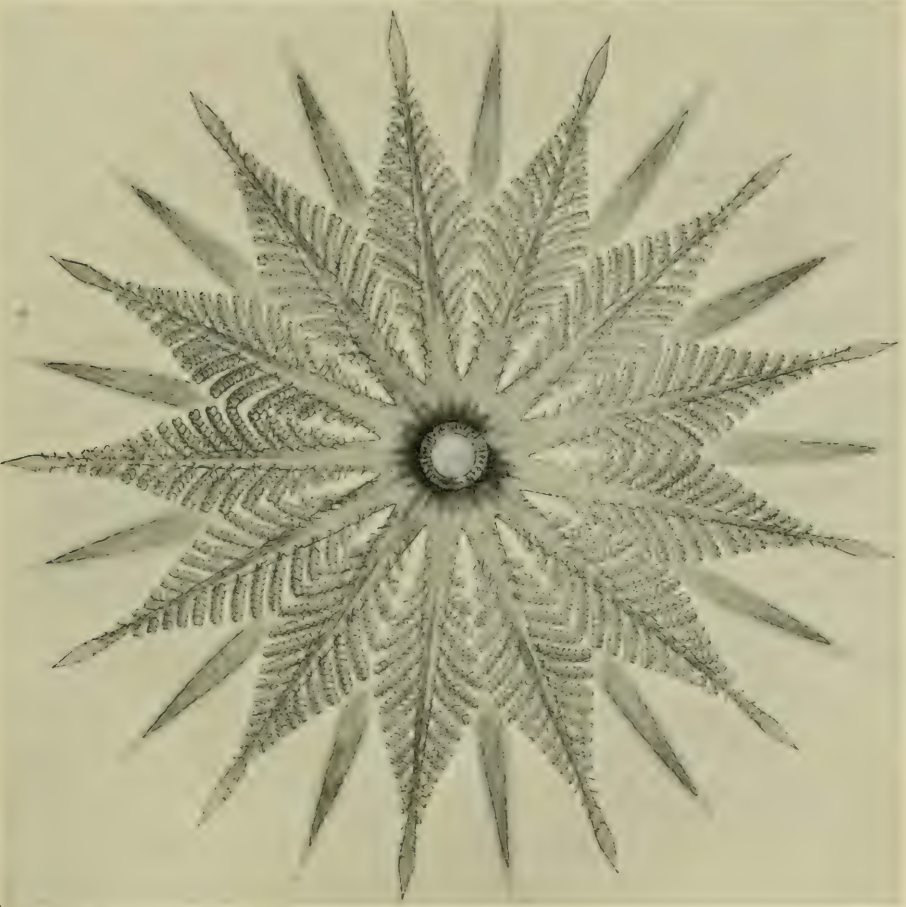


FIG. 128.—*Cycadeoidea ingens*. Plan of the bisexual flower, showing the central ovuliferous cone, the whorl of thirteen compound stamens, united at the base, and bearing synangia on their pinnae, and a series of the hairy bracts. The diagram is about on the same scale as Fig. 127, and shows the flower as it would appear, seen from above, if all its parts were fully expanded. From Wieland.

on the modified fertile fronds of Ferns, where the insertion of the sporangia on the lower surface, usual in the case of unreduced sporophylls, is often departed from. The shortly-stalked synangia are much broader than long, contain two rows of loculi (Figs. 129 and 130), and closely

resemble those of certain Marattiaceae, simulating in a remarkable degree the stalked synangia of *Marattia Kaulfussii*.¹ The analogy of this species, though not of any taxonomic significance, shows that there is no absolute necessity to regard the pedicellate synangia of the Bennettiteae as representing distinct leaflets.

The form of the synangia in *Cycadeoidea* is somewhat

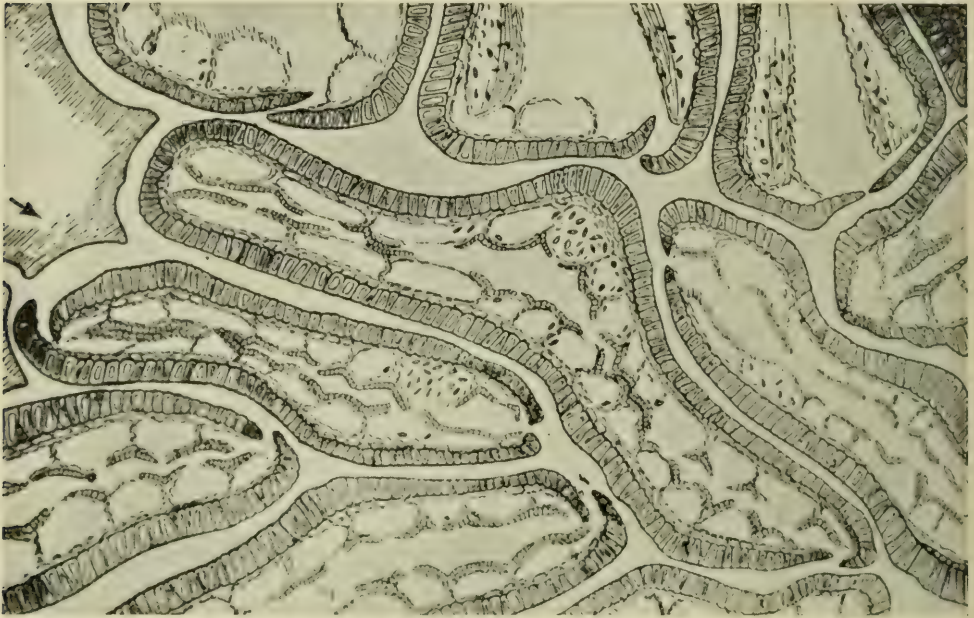


FIG. 129.—*Cycadeoidea dacotensis*. Transverse section through rachis of a sporophyll and adjacent synangia. The middle and lower synangia are cut transversely, the upper very obliquely. The palisade-layer, walls of the loculi, and spores are all shown. \times about 25. From Wieland.

affected by their crowded arrangement in the limited space afforded by the infolded sporophyll (Fig. 129).

The synangia shown in Fig. 129 are for the most part cut transversely, showing the full number (20-30) of the loculi, while Fig. 130 represents a single synangium cut longitudinally through the short stalk, in a plane at right angles to the rows of loculi, so that two loculi only are shown. The exterior of the synangium is formed by a well-developed palisade-layer, thickened near the base

¹ See Christ, *Farnkräuter der Erde*, p. 359, Fig. 1129, 1897.

(Fig. 130); this is lined by a layer of small, thin-walled cells, which also form the inner walls of the loculi (Fig. 129). In dehiscence the two rows of loculi appear to have split apart, the synangium thus opening by two valves, while the individual loculi dehisced by longitudinal slits (Figs. 129 and 130). If this was the case, the resemblance to *Marattia* extended to the mode of dehiscence.

The microspores or pollen-grains have been carefully examined by Dr. Wieland, but without finding any decisive proof of the presence of antheridial cells. In size the microspores are intermediate between those of Cordaiteae and recent Cycads.

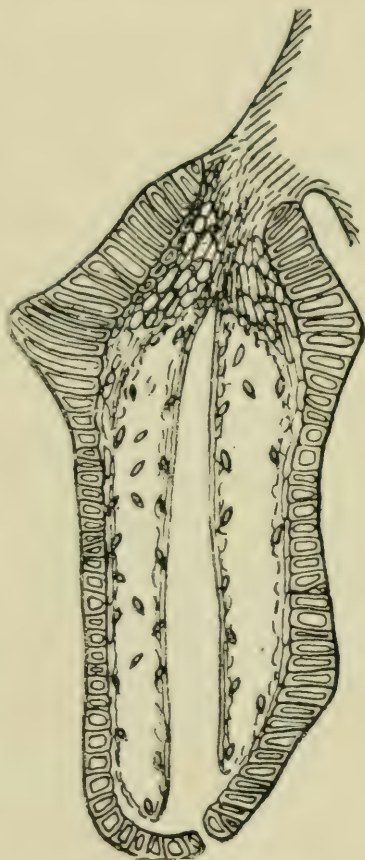


FIG. 130.—Longitudinal section of a synangium, showing short stalk attaching it to rachis. The "buttressing" of the basal part of the wall is shown; also two loculi, in longitudinal section, containing some pollen-grains. Dehiscence appears to have begun. $\times 40$. From Wieland.

Although, as already mentioned, the structure of the flower in both American and European Bennettiteae appears to have been comparatively uniform, some new points of interest have been raised by Dr. Wieland's later observations.¹

In a flower-bud referred to *Cycadeoidea colossalis*, Ward, Dr. Wieland finds that each of the ten stamens bears at the back two prominent flat wings or crests which appear to have extended to the apex of the flower, forming collectively a kind of

¹ See his *American Fossil Cycads*, vol. ii., "Taxonomy," Carnegie Institution, Washington, 1916.

domed summit. This curious complication of the structure may also have occurred, in a certain degree, in other species. The sterile region of the staminal rachis was immensely developed in the case of *C. colossalis*, leaving a rather limited space for the fertile part, bearing the synangia.¹

The question has arisen, whether all Bennettitean flowers were functionally bisexual or whether monoecism, by abortion of one or other organ, may not have occurred in certain cases. The best evidence for the latter condition was found by Dr. Wieland in *Cycadeoidea Jenneyana*, Ward. Here, in a very immature flower-bud, there were thirteen stamens, bearing large synangia already nearly mature. The central receptacle was much elongated, ending in a point, and bore only a very thin ovulate zone, the female organs being so small as to suggest abortion. In a relatively mature ovulate cone on the same stem, with a hemispherical receptacle, the seeds were large enough to have contained embryos, while the pedicels and interseminal scales were well developed. The line of insertion of the hypogynous staminal disc appeared as if completely grown over, and Dr. Wieland infers that it could never have been much developed. He regards this as "a clear case of Cycadeoidean monoecism."² The evidence, however, hardly seems to be decisive, for the differences between the two fructifications may after all be due merely to age. Other cases are less clear, but there is no doubt a possibility that monoecism may have occurred.

Some of the American species of *Cycadeoidea* belong to the same group as the British *Bennettites Gibsonianus*, as shown by the shortened, cushion-like receptacle and other characters. In some of these the bisexual character of the flower has been demonstrated, so that there is a strong presumption that the same was the case in *B. Gibsonianus*, the absence of stamens in the specimens

¹ See Wieland, *l.c.* p. 70.

² Wieland, *l.c.* p. 41.

observed being simply due to the maturity of the fruit at the time of fossilisation. In many of the American fructifications, both young and old, where the stamens were not preserved, Dr. Wieland was able to detect the remains of the staminate disk seated on the rim of the receptacle. Prof. Seward points out that in *B. Gibsonianus* there is no indication of any similar remnant of a whorl of microsporophylls, and finds it difficult to believe that any such fertile leaves ever existed.¹ The negative evidence, however, seems to carry little weight. One cannot expect always to be able to detect the remains of stamens in a ripe fruit, especially in a fossil one.

So far as the Bennettiteae are concerned, the evidence appears to be overwhelming that the flowers generally were morphologically bisexual, and that monoecism, if it ever occurred, was due to the arrested development of organs already present in the bud.

Direct proof of the occurrence of bisexual flowers in European species is not wanting. In a magnificent fossil Cycad, now named *Cycadeoidea Reichenbachiana*, probably of Lower Cretaceous age, preserved in the Zwinger Museum at Dresden, and found as long ago as 1753 near Cracow, Dr. Wieland has demonstrated in some of the flowers the presence of a staminal disk, which in this case consists of sixteen stamens. They appear to be well preserved, though sections have not been cut. The ovulate cones are also present, but Dr. Wieland leaves open the question whether the flowers were functionally bisexual throughout or partly monoecious.² The floral structure appears to agree in all essential respects with that of the American species, *C. dacotensis*.

In a British species, *Bennettites maximus*, Carr, from the Lower Greensand of the Isle of Wight, Dr. Marie C. Stopes has found extremely young fructifications, in

¹ *Fossil Plants*, vol. iii. p. 395.

² See Wieland, *l.c.* p. 123.

which she was able to demonstrate the presence of a whorl of fourteen organs, no doubt the male sporophylls, surrounding the central receptacle; the latter is of a flattened form and bears the immature ovules. These flower-buds appear to be the youngest which have yet been investigated in the family, and so far afford the only example in a British species of the preservation of the bisexual stage.¹

From the comparison of younger and older stages of the flower (as, for example, in *Cycadeoidea dacotensis*) it is evident that as the fruit matured, the expanding gynaecium encroached on, and ultimately filled, the space originally occupied by the whorl of stamens. It has sometimes been maintained that the flowers of the Bennettiteae were proterandrous, the pollen being ripe before the ovules were ready for fertilisation; as we know practically nothing of the structure of the ovules at the fertilisation stage, there have never been any good grounds for this supposition. A recent observation of Dr. Wieland's seems, in fact, to point in the opposite direction.

In describing a young flower-bud of *Cycadeoidea Painei*, he says: "Although the ovulate outlines appear early, the initial synangial growth is late."² Thus, in this case, the ovules seem to have preceded the pollen-sacs in their development.

The probable "monocarpy" of some of the Bennettiteae has already been noticed (p. 343). The term is applied to "Seed-plants which fruit once only in the normal life-time and then die down."³ Five species of *Cycadeoidea* are regarded by Dr. Wieland as more or less

¹ M. C. Stopes, "New Bennettitean Cones from the Lower Cretaceous," *Phil. Trans. Royal Soc. Series B*, vol. 208, 1918.

² G. R. Wieland, "A Study of some American Fossil Cycads: VIII. Notes on Young Floral Structures," *American Journal of Science*, vol. xlvii. 1918, p. 645.

³ G. R. Wieland, "Monocarpy and Pseudo-monocarpy in the Cycadeoids," *American Journal of Botany*, vol. viii. 1921.

completely monocarpic. The best example is the great Hermosa Cycadeoid (*C. Dartoni*), in which the specimen consists of the upper half of a trunk, originally about a metre in height. The remaining portion is wonderfully preserved, and the armour is packed with mature fruits, of which there are not less than five hundred, practically all with ripe embryos. A few may have been abortive, but the specimen strongly suggests that the plant was fruiting all over, and once for all, especially as the leaves at the apex are small and rudimentary, as if the plant were moribund. This wonderful specimen, perhaps the most striking fossil plant known, was found at an isolated locality in S. Dakota.¹

The family Bennettiteae is characterised by relatively short, thick stems, densely clothed with leaf-bases, Cycad-like foliage, and lateral flower-buds, the flowers bisexual, or perhaps sometimes monoecious by abortion, enclosed in bracts; the androecium consisting of a connate whorl of compound stamens, the gynaecium of numerous erect, stalked ovules intermixed with interseminal scales; the seeds exalbuminous or nearly so. Fertilisation was no doubt of the Gymnospermous type, for the micropyles are exposed; whether it was effected by motile spermatozoids or otherwise must remain an open question.

B. *Williamsoniaceae*

Many years before the existence of such a family as that of the Bennettiteae was even suspected, certain remarkable fossils were described from the Lower Oolite of the Yorkshire coast, under the name of *Zamia gigas*.² The fullest account of these fossils is that presented by

¹ G. R. Wieland, *American Fossil Cycads*, vol. ii. chap. vii.

² Lindley and Hutton, *Fossil Flora of Great Britain*, 1830. Originally figured by Young and Bird, *Geological Survey of the Yorkshire Coast*, 1822.

Williamson to the Linnean Society in 1868. Our Fig. 131 (from Williamson's memoir) represents the plant in a restoration which has been proved by more recent in-



FIG. 131.—*Williamsonia gigas*. Williamson's original restoration of the plant, showing the upright stem, with rhomboidal leaf-scars, the crown of *Zamia*-like leaves, and the scaly, spherical fructifications. From the *Linnean Soc. Trans.*

vestigations to be essentially correct. Mr. Carruthers, in his paper on Cycadean stems above referred to, established the genus *Williamsonia* for the reception of *Zamia*

gigas and allied forms, and this name is the one now used.¹

The various organs of the plant are, as usual among fossils, almost always found separately. They consist of the large *Zamia*-like leaves (from which the old generic name was taken), portions of the stem, covered with the rhomboidal leaf-scars, and lastly the fructifications, with the long scaly stalks on which they were borne. Williamson pieced these various parts together, as shown in his restoration, and Brongniart confirmed his conclusions, but other authorities entirely rejected them, regarding the fructifications as those of Monocotyledons, and as having nothing to do with the Cycadean foliage or stem. Williamson's view proved to be the correct one, and his plant has turned out to represent an important family.

The fructification of *Williamsonia gigas* is in size and appearance something like a common artichoke, and was borne at the end of a long stalk, 20 or 30 cm. in length, covered with spirally arranged scale-leaves. The exterior of the globular fructification was formed by the overlapping, involucre bracts. No petrified specimens of this species are known. Consequently, the organisation is difficult to explain, and has given rise to some interpretations, more ingenious than probable, which cannot be discussed here. The established facts appear to be that the ovulate cone had essentially the same structure as in Bennettiteae, but probably had a sterile apex or corona, comparable to that of *Williamsoniella* described below (p. 361). The gynaecium was surrounded by bracts, the whole flower-bud attaining a great size ($4\frac{3}{4}$ inches in diameter, for example).

A male flower or disk, probably referable to this species, has been described by Mr. H. Hamshaw Thomas. It is still uncertain whether the ovulate cone and the

¹ Williamson, "Contributions towards the History of *Zamia gigas*," *Linnean Society's Transactions*, vol. xxvi. (published 1870); Carruthers, *l.c.*, in same volume.

staminate disk formed parts of the same flower, or the sexes were separate, but the balance of evidence seems to incline to the conclusion that the flowers were unisexual.¹

Prof. Seward and others, from the study of a Yorkshire specimen in the Yates collection now at Paris, have proved conclusively that the *Williamsonia* flowers and the *Zamites* leaves were borne on the same stem. The leaves and floral peduncles are shown in connection with the axis.²

The investigations of Nathorst, Halle, and Thomas have brought to light various other species of *Williamsonia* from the Oolite of Yorkshire. Male and female organs are found separate, among the foliage, and have been referred to different species. A staminate flower of *W. spectabilis*, Nathorst, as restored by Mr. Thomas, is shown in Fig. 132, and probably gives a faithful representation of this type of androecium. It is, in this case, of the same general type as the staminate disk of the Bennettiteae. The microsporophylls are fused below into a cup-shaped tube; above, they become free and bend inwards. The free limbs are pinnate, and the slender pinnae bear the synangia. The pinnae are said to have sprung from the midrib and not from the margins of the sporophyll. No bracts are present, unless, indeed, they were completely adherent to the whorl of stamens. In another Yorkshire flower, *W. whitbiensis*, described by Nathorst, the microsporophylls appear to have been simple, each bearing two parallel rows of synangia.

The female cones are in all cases of the Bennettitean type; some are sufficiently well preserved (in a carbonised state) to show clearly the micropyles of the

¹ H. H. Thomas, "On some new and rare Jurassic plants from Yorkshire: the male flower of *Williamsonia gigas*," *Proc. Cambridge Phil. Soc.* vol. xviii. p. 105, 1915.

² Figures of the critical specimen will be found in Wieland, *American Fossil Cycads*, vol. ii. Fig. 64, A, and Seward, *Fossil Plants*, vol. iii. Fig. 541.

seeds among the interseminal scales—as in *W. Leckenbyi*, Nathorst.

Williamsonias have been described from most parts of the world. In the island of Sardinia British species have been recognised. India and Mexico are countries peculiarly rich in such fossils. From the province of Oaxaca, in the south of Mexico, Dr. Wieland has made magnificent collections, including many Williamsonian fructifications, closely associated with the Cycad-like

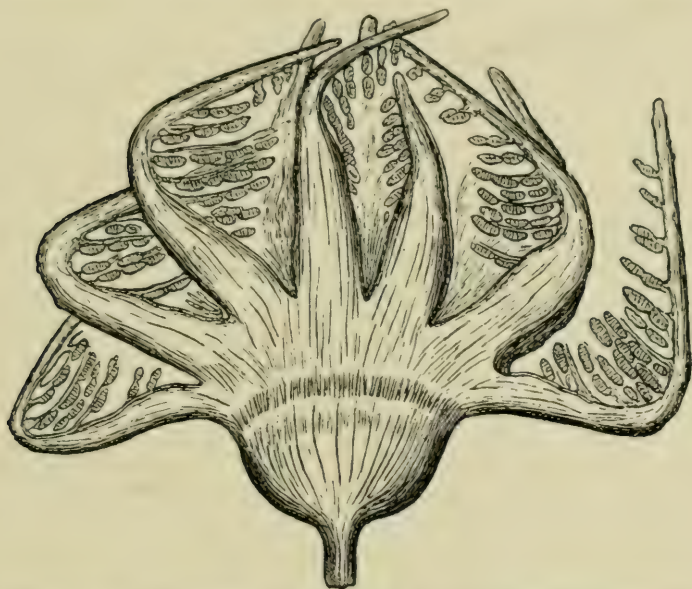


FIG. 132.—*Williamsonia spectabilis*. Restoration of an almost mature male flower, showing the connate sporophylls, with pinnae bearing synangia. Slightly reduced. After H. H. Thomas.

foliage, and sometimes with the stems.¹ The flora is of Liassic age. The female flowers and fruits, enclosed in bracts and sometimes borne on a slender stalk, are frequent. The structure is sufficiently preserved to prove that the gynaecium was essentially like that of Bennettiteae, often with a considerable sterile region of scales only at the base, and sometimes with a sterile apex. Dr. Wieland says that in none of the forms can

¹ See his fine memoir (in Spanish), *La Flora liasica de la Mixteca Alta*, Instituto Geologico de Mexico, 1916, with Atlas of 50 plates. The chief results are incorporated in *American Fossil Cycads*, vol. ii.

it be definitely determined whether an hypogynous staminate disk was present or not.

The most important specimen for the androecium is found in *Williamsonia mexicana*, the famous "El Consuelo Cycad." Here the staminate disk is bell-shaped and about 5 cm. in total length. The greater part is completely connate, the free limbs of the sporophylls being only about a centimetre in length. They are perfectly simple, and each bears two rows of synangia, one on each side of the rachis. Dr. Wieland describes the stamens as "simply pinnate"; this is on the assumption that each synangium represents a pinna, which may or may not be the case. On any view the microsporophylls of this species are remarkably simple compared with those of most Cycadeoideas or of *Williamsonia spectabilis*, while they are comparable in this respect to those of *W. whitbiensis* of the Yorkshire coast. It is noticeable that this simple type of male apparatus occurs in a relatively early representative of the group.¹

Throughout the genus *Williamsonia* we find little evidence of bisexual flowers; male and female organs generally occur separately, and there is thus a certain presumption that the flowers were unisexual, especially as it is difficult to fit the parts together on the opposite hypothesis. One specimen, however, from the Yorkshire coast, now in the Yates collection at Paris, "is evidently from the apical synangial zone of a bisporangiate strobilus of the Cycadeoid type."² Thus it is possible that both conditions may have occurred within the genus.³

¹ For Figures see Wieland, *American Fossil Cycads*, vol. ii. Fig. 81, A; *Flora liasica*, lam. xxii. and lam. xxix. Figs. 1 and 2.

² Wieland, *American Fossil Cycads*, vol. ii. p. 204, Fig. 80, D.

³ Much of our knowledge of *Williamsonia* fructifications, especially those of the Yorkshire coast, is due to Prof. Nathorst. See his "Beiträge zur Kenntnis einiger mesozoischen Cycadophyten," *Kongl. Svenska Vet.-Akad. Handl.* vol. xxxvi. 1902, Stockholm; "Über *Williamsonia*," etc., *ibid.* vol. xlv. 1909; "Neue Beiträge zur Kenntnis der *Williamsonia*-Blüten," *ibid.* vol. xlvi. 1911.

Petrified specimens referable to *Williamsonia* are rare ; considerable interest therefore attaches to a cone, named *Williamsonia scotica* by Prof. Seward, of which the structure is preserved in a silicified condition. The specimen, found at Eathie, Cromarty, was originally described and accurately figured in its external aspect by Hugh Miller, from whose description the following lines are quoted : “ In one of these [cones] the ligneous bracts or scales, narrow and long, and gradually tapering till they assume nearly the awl-shaped form, cluster out thick from the base and middle portions of the cone, and, like the involucral appendages of the hazel-nut or the sepals of the yet unfolded rose-bud, sweep gracefully upwards to the top, where they present at their margins minute denticulations.”¹

The specimen has been fully investigated, by means of sections, by Prof. Seward. Its age, regarded by Hugh Miller as Liassic, is now believed to be much later (Upper Jurassic), though this is somewhat doubtful. The cone is about 11 cm. long by 6 cm. in maximum diameter. The “ minute denticulations ” on some of the bracts, mentioned by the discoverer, are interpreted by Prof. Seward as rudimentary pinnae. A remarkable feature of the cone is the presence of a branch, near the base. The hairy covering consists, not oframenta, but of simple or branched hairs, like those of some recent Cycads. The upper part of the axis forms the receptacle, and is densely covered with ovules and interseminal scales ; thus the gynaecium was of the same type as in Bennettiteae. The cone was at a young stage ; the ovular zone is only about 2 mm. thick. Ovules and interseminal scales are much alike ; the former, however, are somewhat narrower and more cylindrical. Each ovule, which is shortly stalked, is surrounded by five or six of the polygonal scales. In the ovule the nucellus can

¹ Hugh Miller, *Testimony of the Rocks*, Edinburgh, 1857, p. 480.

be distinguished, surmounted by the long micropylar region, with a narrow canal.

There seems to have been no room beneath the gynaecium for any stamens, which, if they existed, ought to have been evident at so young a stage. There is thus a strong presumption that the flower was unisexual. This character favours the reference to *Williamsonia* rather than to *Bennettites*. Neither is it likely, from the habit of the cone, that it was ever enclosed among crowded leaf-bases, as in the latter genus. The specimen may be provisionally accepted as the petrified female flower of a *Williamsonia*.¹

We may now refer to some other genera, provisionally included in the Williamsonian tribe. Mr. H. H. Thomas has described an interesting new genus, *Williamsoniella*,² of which the best-known species is *W. coronata*, Thomas, from the Middle Jurassic (Middle Estuarine Series) of Gristhorpe Bay, Yorkshire. The species is represented by flower-buds, mature flowers, detached microsporophylls, and female organs. Leaves and stems, belonging in all probability to the same plant, have also been recognised.

The flower was borne on a long stalk, and when fully open was a little more than an inch in diameter (see Fig. 133). It was not enclosed in bracts (though detached bracts or bud-scales have been found), and consisted of a whorl of twelve to sixteen free microsporophylls or stamens, surrounding the female receptacle. Each stamen was simple, with a marked longitudinal ridge on the upper surface, bearing the synangia; there were usually six of the latter, three on either side of the median ridge. Each synangium appears to have been

¹ Seward, "A petrified *Williamsonia* from Scotland," *Phil. Trans. Royal Soc. Series B*, vol. 203, 1912. See also his *Fossil Plants*, vol. iii. p. 449.

² H. H. Thomas, "On *Williamsoniella*, a new type of Bennettitalean Flower," *Phil. Trans. Royal Soc. Series B*, vol. 207, 1915.

partitioned into numerous loculi, containing the pollen-grains.

The gynaecium was, broadly speaking, of the type usual throughout the Bennettitales; it consisted of an elongated receptacle, bearing numerous ovules and interseminal scales, closely crowded together (Fig. 133). The most remarkable feature is that the receptacle was prolonged above into a sterile summit, the corona, with fluted sides and sometimes with a terminal appendage. Examination of unopened flower-buds showed that the fluting of the corona was due to the pressure of the tips of the stamens before they opened out.

The ovules possessed no distinct stalks, and have been described as sessile; the interseminal scales are club-shaped; in the mature flower the

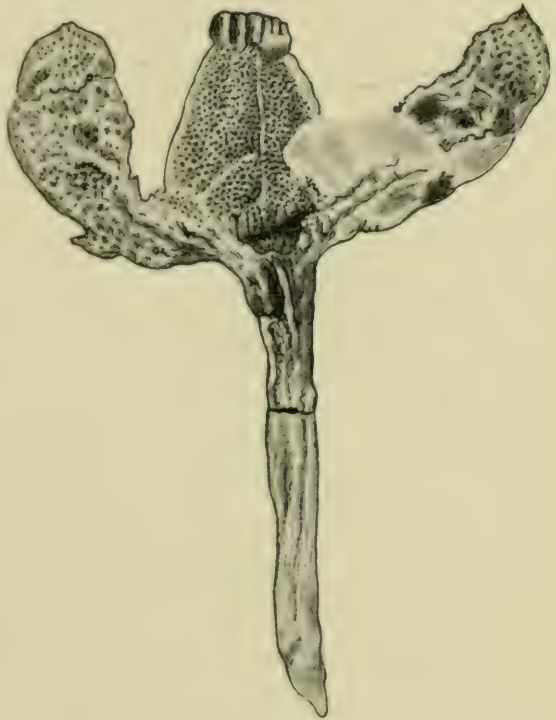


FIG. 133.—*Williamsoniella coronata*. Mature flower, showing peduncle, ovulate strobilus, surmounted by the corona, and microsporophylls attached. $\times 2$. After H. H. Thomas.

long micropyles of the ovules project between the surrounding scales.

Thus the flower of *Williamsoniella* was bisexual, with remarkably simple stamens, not united to a disk, and with a gynaecium characterised by its sterile, crown-like summit. The question arose, to what sort of plant did this fructification belong? In close and constant association with the flowers, Mr. Thomas found numerous

leaves of the form known as *Taeniopteris vittata*, Brongt. —narrow, simple leaves, with a midrib and forked lateral veins (Fig. 134). The stomata of these leaves agree exactly in structure with those found on the stamens of the *Williamsoniella* flower. Thus there is the strongest probability that the leaves and flowers belonged to the



FIG. 134.—*Williamsoniella coronata*. Restoration of part of the plant, showing the forked stem, the supposed *Taeniopteris* foliage (upper leaves removed), and the flowers. The central flower has shed its stamens. About half natural size. After H. H. Thomas.

same plant. Further, in association with both, portions of forked stems were found, of a comparatively slender form. Leaf-scars are met with on the stem, and agree with the scar at the base of a detached leaf.

Thus Mr. Thomas has been able, with much probability though not with certainty, to effect a reconstruction of the plant in all its essential features. Fig. 134 shows the result. It will be seen at once that the habit, as inferred from the available data, was totally unlike

that of a Cycad or a *Bennettites*. The long, slender stems, falsely dichotomous, bore scattered, simple leaves; the stalked flowers were probably produced in the forks. Yet the structure of the epidermis of the *Taeniopteris* leaves agrees essentially with that in the pinnate foliage of evident Cycadophytes. Thus, *Williamsoniella* strongly confirms the opinion that some of the earlier "fossil Cycads" differed widely in habit both from the recent Cycadaceae and from the Bennettiteae of later Mesozoic age.

Mr. Thomas's genus has much in common with a plant from the Rhaetic of Sweden previously discovered by Nathorst, and named *Wielandiella angustifolia*.¹ In this case fructifications have been found, *in situ*, at the forks of the comparatively slender, branched stem. The associated leaves, probably borne in rosettes below the points of forking, are of the *Anomozamites* type, *i.e.* the small frond may be entire or divided into a small number of very unequal segments. There is thus an approach to the simple, *Taeniopteris* form of leaf referred to *Williamsoniella*.

As regards the fructifications, where the gynaecium is preserved it is that of a small *Williamsonia* or *Bennettites*; the micropyles of the seeds, among the interseminal scales, can be clearly recognised, and bracts are also present. In other specimens the club-shaped receptacle is stripped of bracts, seeds, and scales, but around the base there is a palisade-like ring, apparently of very small sporophylls, from which pollen-grains have been obtained. The staminal disk is thus either very rudimentary or very imperfectly preserved. The inference is that the flowers were bisexual, morphologically if not functionally.

The genera *Williamsoniella* and *Wielandiella*, so

¹ See Nathorst's memoir of 1909, above cited, and earlier papers there mentioned. Prof. Seward has re-examined the specimens; see his *Fossil Plants*, vol. iii. p. 463.

different in habit from the typical Cycads, have recently been placed by Wieland in a special family, the Microflorae.¹ The relationship to *Williamsonia* is, in any case, evident.

A fructification, described by Nathorst under the name *Cycadocephalus Sewardi*, is regarded with good reason as belonging to the Williamsonian group. The fossil comes from the Lower Rhaetic of Sweden, and is thus an early example of the family. It is a large flower, 10 cm. long by 7 cm. broad, and consists of a considerable number (16-18) of sporophylls, which are free from one another except at the base. The whole is seated on a stout peduncle. Each sporophyll bears on its inner side two rows of appendages, one row on either side of the midrib. The appendages are slender and about an inch in length. They were found to contain microspores (pollen-grains) in groups. Nathorst regarded the appendages as synangia of enormous dimensions; it is more probable, perhaps, that they represent pinnae bearing synangia. No trace of female organs was found. The specimen thus appears to be a staminate flower of the *Williamsonia* type, but its exact interpretation is doubtful.²

The fossils known as *Weltrichia*, from the Rhaetic of South Germany, are even more obscure, but may probably be of the same nature as *Cycadocephalus*.

Little is known of the vegetative anatomy of the Williamsonian family; some information has, however, been obtained by Dr. Nellie Bancroft from the study of Indian specimens referred to *Williamsonia pecten*. The stem was 5-6 cm. in diameter, and clothed with an armour of leaf-bases. The single compact woody zone with its narrow medullary rays is described as a characteristic

¹ Wieland, "Classification of the Cycadophyta," *American Journal of Science*, vol. xlvii. 1919.

² See Nathorst, "Zur Kenntnis der *Cycadocephalus*-Blüte," *K. Svenska Vetenskaps-Akad. Handl.* vol. xlviii. 1912; Seward, *Fossil Plants*, vol. iii. p. 473.

feature. "The Indian wood, however, shows multi-seriately pitted tracheides like those of recent Cycads, instead of the scalariform type usually occurring in the fossil stems." The structure of the fronds and their pinnae is in general agreement with that found in the Bennettiteae.¹

Dr. Wieland lays great stress on the distinctness of the Williamsonian tribe from the Cycadeoideae (Bennettiteae) and on the importance of the former. The *Williamsonia* type, he points out, was the most plastic and generalised, while the Cycadeoideae were specialised; they are "the stereotyped terminal forms of a side branch from a great plastic and dominant precursor race."² The Williamsonian stem had, as a rule, a fairly compact wood zone (comparable to that of Cordaiteae or Conifers) and was normally slender and branching. On the other hand, the robust stems of *Cycadeoidea*, with their thin wood, immense medulla and heavy armour, "are exceptional to the point of abnormality."³ Dr. Wieland adds that the *Cycadeoidea* stems were no more characteristic in those days than Cactus stems are now, while the small-flowered microphyllous and plastic types (*e.g.* *Wielandiella*) are of far greater importance.⁴

Thus the Williamsonian tribe, in the wide sense, is regarded as representing most nearly the main line of Cycadophyte evolution, while the specialised Bennettiteae are relegated to a lateral position. This view recognises the fact that, on the whole, the more ancient Mesozoic Cycads are Williamsonian, the later Bennettitean. The separation of the Microflorae (*Williamsoniella* and *Wielandiella*) as a distinct family⁵ does not materially affect

¹ Nellie Bancroft, "On some Indian Jurassic Gymnosperms," *Trans. Linn. Soc. London*, 2nd Series, *Botany*, vol. viii. 1913.

² *American Fossil Cycads*, vol. ii. p. 178.

³ *L.c.* p. 191.

⁴ *L.c.* p. 225.

⁵ See Wieland, "Classification of the Cycadophyta," *Amer. Journal of Science*, vol. xlvii. 1919. The scheme developed in this paper is too elaborate to be reproduced here.

the position, for these genera are clearly of the Williamsonian cycle, and indeed may be said to represent that type in its most extreme and least Cycad-like form.

The geological history of the whole class is thus summed up by Dr. Wieland. "The Cycadeoids [*i.e.* the Bennettitales as a whole] first become dominant Seed-plants in the Lunz of Austria (Keuper) [Triassic] and so continue to the close of the Wealden. They thus typify the Jurassic, about equally overlapping the beginning and close of that period. In the Rhaetic the Cycadeoids first reach notable proportions; they culminate in numbers in the lowermost Lias of Oaxaca and begin to decline in the Wealden, few being left in the Upper Cretaceous." ¹

2. CYCADALES.—Side by side with the Bennettitales, true Cycadaceae, or closely allied plants, probably existed in Mesozoic times, but the evidence for their presence is scanty in the extreme.

Male cones, of a Cycadean type, have been recorded under the name of *Androstrobus*, as, for example, *A. Nathorsti*, a species from the Wealden of Sussex, described by Prof. Seward.² The thick axis of this cone bears spirally arranged, more or less triangular scales or sporophylls, 1 to 1.5 cm. in length. "Towards one end of the specimen the basal part of a scale is seen in surface view, and on it are clearly preserved what are taken to be the outlines of pollen-sacs. . . . The striking regularity with which these impressions are arranged is much more marked than in the pollen-sacs of recent Cycads. On the lower surface of a staminal leaf of *Dioon* or *Encephalartos* we find, on the removal of the pollen-sacs, a fairly distinct reticulate marking, but of much less regularity than in the fossil." ³ From the evidence of this specimen and one or two similar fossils, it has been

¹ *American Fossil Cycads*, vol. ii. p. 214.

² *Fossil Plants of the Wealden*, Part ii. p. 110.

³ Seward, *l.c.* p. 111.

inferred that male cones, not essentially different from those of living Cycads, occurred in Mesozoic floras. The evidence, however, is not wholly convincing, and was considerably shaken by Nathorst's discovery that a cone originally described by him as *Androstrobus Scotti*, and referred to Cycadaceae, was in reality a Lycopodineous fructification with megaspores, for which he created the new genus *Lycostrobus*.¹

As regards female cones of the Cycadaceae, such as are characteristic of the recent sub-order Zamieae, the fossil evidence is unsatisfactory. Various species of *Zamiostrobus* have been described; it is quite probable that cones of this affinity really occur in various Mesozoic deposits, but, generally speaking, the state of preservation of such specimens is so poor that it is impossible to distinguish them with any certainty from Coniferous strobili of similar habit.²

We have already seen (Chapter III., p. 238) that fructifications, possibly referable to Cycadophyta, occur even in the Permian beds, though their true affinity is an open question.

The recent genus *Cycas* differs entirely from other members of the Order in the structure of the female fructification. The carpels are among the most characteristic of vegetable organs, and fossils resembling

¹ A. G. Nathorst, "Paläobotanische Mitteilungen. 3. *Lycostrobus Scotti*," *Kongl. Svenska Vetenskaps-Akad. Handl.* vol. xliii. No. 3, 1908.

² Cf. Seward, *Fossil Plants of Wealden*, Part ii. p. 113. One of the most perfect specimens attributed to the Zamieae is the *Beania gracilis* of Carruthers ("On *Beania*, a New Genus of Cycadean Fruits from the Yorkshire Oolites," *Geol. Mag.* vol. vi. 1869), which consists of an elongated axis, bearing a number of peltate sporophylls, on each of which two seeds are inserted. The sporophylls themselves agree closely with those of a recent *Zamia*, but they are much more remote from each other than in that genus. Prof. Seward was once inclined to regard *Beania* as more probably belonging to Ginkgoaceae than to the Cycads, but has since modified his opinion. See Seward and Gowan, "The Maidenhair Tree," *Annals of Botany*, vol. xiv. 1900. Also Seward, *Jurassic Flora*, Part i. 1900, p. 272; *Fossil Plants*, vol. iii. p. 502.

them have been recorded from various Mesozoic strata; e.g. from the Lias of Mexico. In another case (*Cycadospadix Hennoquei*, Saporta, from the Lower Lias of Metz) the carpel, fimbriated like that of *Cycas pectinata*, bears the scars of the seeds.¹ The evidence for the existence of near allies of *Cycas* in Mesozoic times so far seems strong, but, on the other hand, much doubt has recently been cast on the nature of the leaves referred to *Cycas* or *Cycadites*, with which the carpels are sometimes associated. Nathorst² showed that in several species from the Cretaceous of Greenland, formerly placed in the genus *Cycas*, the vascular bundle of the pinna was not single, as in the recent genus, but double, and that the distribution of the stomata was also quite unlike that in *Cycas*. He therefore placed these forms in a new genus, *Pseudocycas*, and no longer regarded them as belonging to the same sub-order as *Cycas*. It is probable that the species now placed in *Cycadites* may prove to have similar peculiarities.³

The genus *Cycadocarpidium*, Nathorst, is of interest in connection with fossil Cycadales. It consists of cones, compared to those of *Zamia*, but differing greatly in the fact that each sporophyll has a long, foliaceous, ovate or lanceolate lamina; at the base of the leaf-blade two seeds are inserted, accompanied, in one species, by appendages, which may be interpreted either as cupules or as pinnae. These fructifications probably belonged to the vegetative organs known as *Podozamites*, Braun. The nature of the latter genus has been much disputed, but it is now believed to represent leafy stems, the slender

¹ See Saporta et Marion, *L'Évolution du règne végétal : Les Phanérogames*, t. i. p. III, fig. 59, A, 1885. A seed is figured *in situ*, but this is probably a restoration.

² A. G. Nathorst, "Paläobotanische Mitteilungen, 1. *Pseudocycas*," *Kongl. Svenska Vetenskaps Akad. Handl.* vol. xlii. No. 5, 1907. The cuticle of carbonised specimens was examined microscopically.

³ For the present position of this question see Seward, *Fossil Plants*, vol. iii. p. 558; and for fossil Cycadales generally, pp. 496-506.

axis bearing simple leaves, spirally, or sometimes distichously, arranged. The habit has been compared to that of the recent Araucarian genus *Agathis*.

It is still uncertain whether *Podozamites* and the associated *Cycadocarpidium* should be referred to Cycadales or Conifers; in any case the leafy cones would seem to represent a somewhat primitive type of female strobilus. These fossils are essentially of Rhaetic and Jurassic age, and have an almost world-wide geographical range.¹

Both male and female fructifications, possibly of Cycadales, have recently been described by Krasser, from the Lunz (Trias) of Austria. *Lunzia* is a new genus founded for pinnate microsporophylls bearing numerous septate "anthers" on the inner surface. *Pramelreuthia* is a lax cone; the long-stalked microsporophylls, with pollen-sacs on the lower side, recall the *Crossothecas* of the Coal-measures.

Haitingeria, on the other hand, consists of deeply pinnatifid megasporophylls, bearing numerous seeds on the edges of the segments; these organs have been compared with the carpels of *Cycas*.²

At present the whole question of the existence of Mesozoic Cycadales, whether of the sub-order Zamieae or Cycadeae, is in an unsatisfactory position and the positive evidence singularly meagre. There are a great number of Cycad-like fossil remains (including isolated seeds), known only as impressions and casts, the true nature of which must remain doubtful until specimens showing structure come to light. At present such specimens, of Mesozoic age, are almost wholly limited to the Bennettitales.

3. AFFINITIES OF MESOZOIC CYCADOPHYTA.—The Cycadophyta of Nathorst form a main subdivision of

¹ Nathorst, "Paläobotanische Mitteilungen," 10, *Kongl. Svenska Vetenskaps Akad. Handl.* Band 46, 1911; Seward, *Fossil Plants*, vol. iv. 1919, p. 447.

² Gothan, *Potonié's Lehrbuch*, 1921, p. 270.

the Gymnosperms, including the Cycadales, the Bennettitales, and no doubt other groups which we are not yet in a position to characterise. The Cycadales correspond essentially to the Order Cycadaceae, with the two well-known sub-orders Cycadeae and Zamieae; the Bennettitales include the Bennettiteae and the Williamsonieae, as above described.

Throughout our description of the Bennettitales we have assumed that these plants really had affinity with Cycads. The sum of their vegetative characters can leave no doubt that this supposition is justified, but it is a striking fact that in their reproductive organs—that is to say, in the very characters on which systematists are accustomed to rely—the Bennettitales differ *toto coelo* from the Cycadaceae. The organisation of the flower is so different from that of the cones of any recent Cycad that it is difficult to determine with any certainty the homologies of the parts in the two groups. It is of course possible that future palaeontological discoveries may reveal the existence of types of fructification intermediate between those of Cycadales and Bennettitales; at present, however, it seems as if their development had followed different lines from a very early stage.

The points in which Bennettitales, especially the Bennettiteae, agree with Cycadales are the form and general structure of the stem, the histological details of its tissues, the arrangement of the leaves, their form and minute structure; in all these respects the agreement is close, so far as the existing investigations on American and European species enable us to judge. The only differences worth mentioning, in the vegetative organs, are the simpler course of the leaf-trace bundles in Bennettitales, and the presence, in most cases, oframenta like those of Ferns, instead of the woolly hairs of Cycads. In these two respects the Bennettitales have been considered more primitive than the sister class. It has been suggested by Dr. Wieland that in Triassic times

there may not yet have been any definite border-line between the two classes, so far as vegetative features are concerned.¹ The Williamsonian tribe, however, if we include the Microflorae, shows a distinctly less close agreement with Cycadales. In *Wielandiella angustifolia*, the oldest known member of the Bennettitales, the habit was equally unlike that of typical Cycadaceae and of typical Bennettiteae, and the same applies to *Williamsoniella*. It has been suggested that an abortive bud occurring beneath the peduncle of the cone in the recent Cycad *Dioon* is the second lateral branch of the primitive dichasium, an interpretation which would tend to bring the Cycadaceous morphology a step nearer to the type of *Wielandiella* and *Williamsoniella*.²

On the other hand, the fructifications are on a far higher level of complexity in the Bennettitales than in the recent group. The lateral, probably axillary, position of the fertile shoots (flowers) may be noted as characteristic of the family Bennettiteae. As Dr. Wieland put it in 1906, the Bennettiteae seized on the lateral bud as a means of fructification, thus ensuring the production of more numerous strobili. In the Williamsonieae, however, the arrangement was quite different. That the axis of the inflorescence is a modified branch of the stem is clear; the enveloping bracts are, no doubt, modified leaves or possibly leaf-bases, and likewise present no difficulty. We might well compare them to the scale-leaves in which the young cone of an ordinary Cycad is enwrapped. It is when we come to the internal organs of the fructification—the stamens, the seed-pedicels, and the interseminal scales—that difficulties begin.

There appears to be no doubt as to the morphological

¹ *American Fossil Cycads*, i. p. 228. The author gives a very full comparison between the two groups, as regards both vegetative and reproductive characters, in his chapter ix. His later views will be found in his second volume.

² F. W. South and R. H. Compton, "Anatomy of *Dioon edule*," *New Phytologist*, vol. vii, Dec. 1908, p. 225.

nature of the stamens, which are clearly sporophylls of a leaf-like and often highly complex character, borne directly on the axis of the fructification. So far, then, as the androecium is concerned, the Bennettitalean strobilus is admittedly a *flower*. The organs of the gynaecium, however, have received various interpretations, which may be grouped under two heads. Either all the organs (seed-pedicels and interseminal scales) are of a foliar nature, in which case the fructification throughout is comparable to a flower, or the seed-pedicels are axial structures,¹ and this part of the fructification is an "inflorescence." The question is important on account of the comparison with the Angiosperms, on which much stress has been laid by recent writers. We will first consider the second view, of which Prof. Lignier was the chief advocate. On his interpretation the interseminal scales are modified leaves, homologous with the bracts, and ultimately with the foliage leaves, while each seed-pedicel is a sporophyll borne on a unifoliar bud, which is probably axillary to an interseminal scale. Prof. Lignier pointed out the analogy which, on his view, existed between the strobilus (or rather the female part of it) and the vegetative stem, in which also only a minority of the leaves have buds (usually fructifications) in their axils. The unifoliar bud, which would thus represent a female flower, is assumed to be extremely reduced.² The analogy with the main stem is the strongest point in this interpretation, but it appears to be open to three serious objections: (1) There is no structural evidence that the seed-pedicel is a bud, or an axial structure of any kind; ³ (2) neither is there any evidence that the

¹ The third view mentioned as possible by Count Solms-Laubach, that the interseminal scales are also axial, does not seem to be upheld.

² O. Lignier, "Le Fruit des Bennettitées et l'ascendance des Angiospermes," *Bull. Soc. Bot. de France*, ser. iv. t. viii. 1908.

³ Unless it be found in the somewhat deeper insertion of the interseminal scales as compared with the pedicels—a very dubious indication. See Wieland, *l.c.* vol. i. p. 118.

pedicels are axillary to certain of the interseminal scales ; (3) there is no known structure among the Cycadophyta or Pteridospermeae from which such an organ as the supposed unifoliar female flower could have been derived by reduction. In an earlier work¹ Prof. Lignier supported his interpretation by a comparison with certain fructifications of Cordaiteae, in some of which, as already mentioned, the seeds were borne at the ends of long peduncles. The analogy, however, is of little value, for the two families are so far apart that their common origin was probably too remote to have led to any community of floral characters. On the whole, the axial theory of the seed-pedicels, though supported with much ingenuity, appears, so far as our present knowledge shows, to lack an adequate structural or comparative basis.

On the alternative hypothesis, all the organs constituting the gynaecium are of the nature of leaves, and borne, in accordance with the observed facts, directly on the axis. Dr. Wieland regards as most tenable "the theory that the seed-pedicel and the interseminal scale are greatly reduced sporophylls analogous to and derived from sporophylls like those of the existing Cycads."² Arber and Parkin, who likewise regarded the whole fructification as a flower, or "anthostrobilus," to use their own term,³ considered that the interseminal scales are "homologous with the carpels of the Angiosperms, despite the fact that they subtend and do not bear the seed-pedicels."⁴ They pointed out "a possibility that the seed-pedicels may, in part, represent a lobe of the carpellary leaf,"⁵ and that they may or may not be homologous with the funicle of Angiospermous seeds.⁶

¹ *Structure et affinités du Bennettites Morierei*, 1894, pp. 68 and 72.

² *L.c.* p. 321.

³ They applied the term "pro-anthostrobilus" to the Bennettitean flower, to indicate its primitive features.

⁴ *Origin of Angiosperms*, p. 59.

⁵ *L.c.* p. 66.

⁶ *L.c.* p. 65.

Prof. Lignier argued with considerable force against the suggestion that seed-pedicels and interseminal scales represent lobes of the carpellary leaves, pointing out the complete independence of the bundles supplying the two organs, the absence of any definite relation in their arrangement, the differences in their structure, and especially the fact that in *Bennettites Morierei* the outer interseminal scales have several vascular bundles and are flattened like the bracts.¹ It seems better to take the view that the interseminal scales are, like the bracts, modified leaves, though much more reduced, while we regard the seed-pedicels as the reduced megasporophylls or carpels. The interseminal scales *may* be sterile carpels, though the transitional forms between scales and bracts are against it. On the other hand, Mr. Thomas has found in the case of his *Williamsoniella* some indications of a type of structure intermediate between a megasporophyll and an interseminal scale. On the view here provisionally adopted, the whole lateral axis constituting the flower may be compared to the main axis of a *Cycas*, or rather to that of a hypothetical Cycadophyte or Pteridosperm bearing both male and female sporophylls, the leaves adjacent to the sporophylls being reduced, as are the scale-leaves of *Cycas*. The bracts are but little modified, while the stamens fully retain their foliar characters, and have been well compared by Wieland to the megasporophylls of *Cycas*. The interseminal scales and the monospermic carpels have undergone a somewhat extreme reduction, and their arrangement appears very different from that of the whorled stamens, though a verticillate order may possibly yet be traced in the organs of the gynaecium. The reduction demanded by the carpellary theory is of course far less than that

¹ O. Lignier, *Le Fruit des Bennettitées*, 1908, p. 7; "Notes complémentaires sur la structure du *Bennettites Morierei*," *Bull. de la Soc. Linn. de Normandie*, sér. v. vol. xiii. 1904. I have occasionally observed interseminal scales with two bundles in *Bennettites Gibsonianus*.

which the axial theory of the pedicel requires ; on the latter view each monospermic pedicel would be the homologue, not merely of a carpel, but of an entire strobilus.

As compared with the seed of a Pteridosperm or Cycad, that of the Bennettitales is considerably simplified, especially in its vascular system, which appears to be almost limited to the chalazal disk or socket. This reduction is no doubt correlated with the enclosure of the seeds in a fruit.

Our knowledge of the earlier Cycadophyta is at present quite insufficient to enable us to form any conception of the course of evolution of the Bennettitalean flower. The recent discoveries of Triassic Cycadophytes, when better known, may be expected to throw some light on the question. Unfortunately our accurate knowledge of the structure of the Mesozoic Cycads, though of extraordinary interest and value, is still to a great extent limited to a comparatively narrow group—a special family which had attained a leading position in those days, somewhat as the Compositae have in the recent Flora. The Williamsonieae diverge widely, in various respects, from the Bennettitean type, but in their case we still have comparatively little knowledge of the internal structure.

The discovery of the bisexual nature of the flower and the arrangement of its parts in the family Bennettiteae greatly strengthened the Angiospermous analogies which had previously been traced. The evidence seems to indicate that in the Williamsonian tribe, on the whole an older race than the Bennettiteae, unisexual flowers were frequent, though in *Williamsoniella* and in *Wielandiella*, the oldest of all, the flowers were no doubt bisexual. We are not, however, as yet in a position to decide whether the similar floral organisation in the Bennettitales and the Angiosperms should be regarded as homologous

or as merely convergent. The question will be further discussed in the concluding chapter.

As regards affinities in other directions, the relation to the Cycadales has always been recognised. Dr. Wieland has repeatedly stated his conviction that the Cycadeoideae (Bennettitales) were true Cycads, though he no longer includes them, as he previously did, in "Cycadales." The Cycad affinity is shown solely in the vegetative characters, and it is remarkable that in some of the oldest Bennettitales the resemblance is much less marked than in their later representatives. If we are guided by reproductive characters, as is the usual practice in taxonomic questions, the two groups appear absolutely different.

The Bennettitalean fructifications have the nature of flowers, giving rise to fruits, while those of Cycadales (apart from the female *Cycas*) are simple cones. The former are commonly bisexual, the latter always dioecious. In the former the stamens form a single whorl, in the latter they are disposed in many cycles on the elongated axis of a cone; in Bennettitales each stamen is foliaceous and often highly compound, in Cycadales it is a simple scale. Where the stamen in the former is of a simple form, the pollen-sacs are borne on the upper surface, in Cycadales always on the lower. The Bennettitales have compound synangia, the Cycadales simple pollen-sacs.

As regards the female organs, the interseminal scales of the Bennettitales are entirely absent in the recent group. In the former, each (much disguised) carpel bears a single terminal ovule; in the latter the carpel bears two (or in *Cycas* more) marginal ovules. In Bennettitales the seed is comparatively small, with a poor vascular supply; in Cycadales it is large and elaborate, with a complex vascular system, like a Palaeozoic seed. In the former the seeds are practically exalbuminous, the embryo filling the cavity; in the latter the seed is highly albuminous with a relatively small embryo.

In fact, the reproductive organs differ from each other in every point, and, except that both groups are gymnospermous, their fructifications have nothing in common. No discovery yet made tends to bridge the gulf between them.

In the family Bennettiteae, the stamens, while in their arrangement and monadelphous fusion they suggest the androecium of a fairly advanced Angiosperm, correspond in form and structure to the sporophylls of a fern. It may, however, be pointed out that in the older group Williamsonieae the microsporophylls very often have a much simpler form. Such stamens are commonly spoken of as reduced, but we have no proof that this was the case. The synangia quite recall those of some recent Marattiaceae. It is, however, altogether improbable that such Fern-like characters (among which the ramenta may also be reckoned) came to the Bennettitales from any group of true Ferns. It is far more a case of parallel development; the Cycadophyta presumably trace their descent through the Pteridosperms, and, as we have seen, it is improbable that the latter were ever derived from Ferns as we now understand them. The Seed-plants must have formed a distinct phylum from very early days.

The Bennettitales certainly present an extraordinary combination of characters—Pteridospermous, Cycadean, and Angiospermous, with great peculiarities of their own; we have no clue to their origin (beyond the general Pteridospermous hypothesis); in the other direction, however, they may throw some light on the important and obscure problem of the descent of the higher Flowering Plants.

II. CONIFERAE

The question of the origin and early history of the Coniferae, now the predominant Order of Gymnosperms, is clearly one of the most important on which fossil botany may be expected to throw light. At present,

however, the evidence on these points is imperfect, so that, though Coniferous remains are abundant enough, it has been said that "no branch of palaeobotanical research makes greater demands upon the patience and self-control of the student."¹ Of late years much progress has been made, but the Coniferae are still, in the present state of our knowledge, unsuited for full treatment in the present course, as any adequate account would far exceed our limits. One or two points, however, may be briefly referred to.

The Coniferae are evidently of great antiquity, for remains which can only be referred to this Order have been found with certainty in the Permian and even in earlier Palaeozoic strata. An interesting Permian and Upper Carboniferous genus, unfortunately still imperfectly known, is *Walchia*, leafy twigs of which are common fossils, while some specimens have been found in fructification. The habit of these branches, of which several species have been described, is quite like that of some of the recent *Araucarias*, such as the Norfolk Island Pine, *A. excelsa*. Certain curious fossils, long described as a distinct genus, under the name of *Tylodendron* or *Schizodendron*, have turned out to be casts of the medullary cavity of stems, probably, in some cases, identical with those of *Walchia*, to which they would thus stand in precisely the same relation as that of the *Sternbergia* casts to the stem of *Cordaite*s. The casts are marked with a characteristic areolation, corresponding to the course of the primary vascular bundles, and agree wonderfully closely with the configuration of the pith in the recent genus *Araucaria*. The structure of the wood surrounding the pith of *Tylodendron* is sometimes preserved, and is found to be of an *Araucarioxylon* type, known as *A. Rhodeanum*, differing from the Cordaitean wood in

¹ Seward, *Fossil Plants*, vol. iv. p. 165, 1919. This volume contains a full and admirable account of the fossil Conifers, compared with the recent types.

the arrangement of the pits and some other trivial characters.

Unfortunately, our knowledge of the *Walchia* fructifications does not go much beyond their external features. On certain specimens small scaly cones are borne, some of which were probably male, while others are known to have been female; in *Walchia filiciformis*, Zeiller¹ showed that each scale of the female cone bore a single seed, an important Araucarian character. In a specimen described by Renault, on the other hand, the lateral twigs each terminate in a bud-like body apparently containing a solitary seed,² though this is doubtful (*Walchia frondosa*, Ren.). On the evidence available there appear to be good grounds for referring such species as *W. filiciformis* to the Araucarieae; the essential character of the latter lies in their fructification, and especially in the carpellary scales, each of which, in the recent members of the family, bears one ovule directly, without the intervention of a seminiferous scale. In vegetative characters there is also considerable agreement, but it appears most probable that under the name *Walchia* distinct generic types have been confounded. It has been maintained that Araucarieae are the oldest tribe of Coniferae; this statement, in the first instance, no doubt depended largely on confusion between Cordaiteae and Araucarieae; the former group is now excluded from the question, but there is some evidence, as we have seen, that in the Permian period Conifers resembling Araucarieae both in vegetative and reproductive characters already existed.

The evidence for the antiquity of the Araucarieae has recently been summed up by Prof. Seward.³ In

¹ *Bassin houiller et permien de Brive, Flore fossile*, 1892, p. 99, Plate xv.

² Renault, *Flore fossile d'Autun et d'Épinac*, Part ii. p. 357, Plate lxxviii.

³ Seward and Ford, "The Araucarieae, Recent and Extinct," *Phil. Trans. Royal Soc. B*, vol. 198, 1906, p. 370; *Fossil Plants*, vol. iv. p. 301, 1919.

Triassic, Rhaetic, and Liassic beds there are a number of specimens of twigs, wood, and cones which may probably be Araucarian; by Rhaetic times the family was in all probability established. From the Jurassic onwards the evidence, from well-preserved cones and other remains, is ample and convincing, showing an almost cosmopolitan distribution. It is interesting to find that examples of probable Araucarieae with more than one seed on the carpellary scale have recently been described from Cretaceous horizons. In the genus *Protodammara*, of Hollick and Jeffrey, from the State of New York, there are three seeds on each scale, while the anatomical structure indicates a relation to the recent genus *Agathis*.¹ In the *Pseudoaraucaria* of Fliche, from the Albien of the Argonne, each scale bears two seeds, and the structure suggests a possible link between the Araucarieae and the Abietineae.

The Taxodieae, the tribe to which the famous "Big Trees" of California (*Sequoia gigantea*) belong, may claim a high antiquity, if the genus *Voltzia*, from the Upper Permian and Triassic, is rightly referred to this group. The evidence in this case does not depend merely on vegetative characters, but is strengthened by the morphology of the cone, the seminiferous scales of which are lobed, as in the recent genus *Cryptomeria*. It is not, however, certain that the scales were double, as in Taxodieae. *Voltzia* has also been regarded as an Araucarian. A number of other fossil remains have been referred to the Taxodieae, but they are for the most part of Tertiary or Cretaceous age. Cones closely resembling those of *Sequoia*, attached to leafy branches of the type known as *Brachyphyllum*, have, however, been described by Zeiller from beds referred to the Upper Lias of Madagascar.

¹ A. Hollick and E. C. Jeffrey, "Affinities of Cretaceous Plant Remains commonly referred to *Dammara* and *Brachyphyllum*," *American Naturalist*, vol. xl. 1906.

As regards remains of the Abietineae, the fossil cones are seldom well enough preserved to show the seeds in relation to the seminiferous scale, the character on which the identification of the tribe depends. There is some evidence, from characteristic winged seeds and foliage shoots, for the existence of Abietineae as early as the Rhaetic. In *Schizolepis* the leafy shoots are much like those of a Pine. In the case of such a genus as *Pinus* the grouping of the needles on short twigs is so characteristic as to leave little doubt of the affinity, when this feature is associated with a resemblance in the habit of the cones. It has been known for some time that Abietineae, allied to *Pinus*, occurred in the Wealden formation; the evidence is strengthened by the occurrence of Abietineous wood at the same horizon.¹ The genus *Pinus* has been recognised, on the evidence of characteristic cones, in the Portlandian (Upper Oolite), while Abietinean wood has also been found in deposits of Jurassic age. Prof. Jeffrey has described, under the name of *Prepinus*, leaves and twigs of a Cretaceous Conifer, preserved as lignite, which, while showing clear indications of affinity with *Pinus*, possess centripetal xylem in the foliar bundle, and other primitive characters, even recalling the structure of Cordaitan leaves to some points. Jeffrey regards *Prepinus* as a probable ancestor of the true Pines.² The leaves are needle-like, and are numerous on each of the short shoots.

Cupressineae have not been traced with certainty very far back, though twigs and cones of Cupressineous habit occur in the Jurassic. A fossil species of the recent genus *Callitris* (*C. Reichii*) has been described from the Upper Cretaceous of Moravia, and seems to be an excep-

¹ Seward, "Plants of the Wealden," Part ii. p. 193; "On a New Species of Conifer, *Pinites Ruffordi*," *Journal of the Linnean Society*, vol. xxxii. p. 417, 1896.

² E. C. Jeffrey, "On the Structure of the Leaf in Cretaceous Pines," *Ann. of Bot.* vol. xxii. 1908.

tionally clear specimen, with characteristic cones of both sexes well preserved.¹ If a recent genus already existed, in a characteristic form, in Cretaceous times, it is certain that the group to which it belongs must have been of very considerable antiquity, but we can only look to future discoveries for further light on its history.

The Taxaceae (taken, in a wide sense, to include the Podocarpeae) have not been traced back with certainty to a lower horizon than the Cretaceous, though branches with leaves like those of the genera *Cephalotaxus* and *Podocarpus* have been described from earlier strata; e.g. the Potomac formation, probably of about Wealden age. Nathorst² showed that his genus *Stachyotaxus*, of Rhaetic age, has much in common with *Dacrydium*, though in the fossil there are two seeds to each carpellary scale, instead of one. He further suggested the possibility that the contemporary *Palissya*, with five or six pairs of cupulate seeds on each carpel, may be related, though he pointed out as an alternative view that these genera may belong to an extinct race of Gymnosperms, intermediate between Coniferae and Cycadophyta.

Coniferous wood, in a petrified, and especially in a silicified condition, is among the commonest fossils of the Mesozoic strata. Such specimens, for example, are most abundant in the Lower Greensand and Wealden of the Isle of Wight, and in the Purbeck beds of Eastern Dorsetshire. Often the preservation is absolutely perfect, so that the finest details of histological structure

¹ *Potonié's Lehrbuch der Paläobotanik*, 2nd edition by Gothan, 1921, p. 323, Fig. 71. The student will find an excellent summary of the geological history of the Coniferae in this text-book. See also Zeiller, "Les Progrès de la paléobotanique de l'ère des Gymnospermes," *Progressus Rei Botanicae*, Bd. ii. 1907.

² "Paläobotanische Mitteilungen. 7. Über *Palissya*, *Stachyotaxus*, und *Palaeotaxus*," *Kongl. Svenska Vetenskaps Akad. Handl.* Band xliii. No. 8, Dec. 1908.

can be studied.¹ A very exact knowledge of the structure of recent Coniferous wood is necessary, in order to determine with any certainty the particular family to which a given fossil specimen belonged. Recent investigations of Dr. Gothan² and others, in which additional characters, and especially the details of structure of the medullary rays, are taken into account, have greatly advanced this difficult subject.²

The study of the fossil Coniferae is not yet sufficiently far advanced for us to decide which of their families is the most ancient, or to form any clear conception of the course of their evolution. The direct palaeontological evidence, however, apart from theoretical considerations, is favourable to the opinion that the Araucarieae have the longest fossil history, probably overlapping that of the typically Palaeozoic family Cordaiteae. The subject will again be referred to in the final chapter.

The discovery of fresh sources of evidence from remains with structure preserved, as in the case of the Cretaceous lignites of the eastern United States, investigated by Prof. Jeffrey and his colleagues, is throwing much new light on the geological record of the Coniferae.

III. GINKGOALES

That isolated type, the genus *Ginkgo*, now regarded as constituting an Order, or even Class, by itself, has proved to be of great antiquity. Here we have to do with a well-characterised, easily recognised group, and the palaeontological evidence is consequently of great significance.

¹ See Barber, "*Cupressinoxylon vectense*," for an especially careful and detailed examination of a Mesozoic Coniferous wood, *Annals of Botany*, vol. xii. 1898.

² For summaries, see W. Gothan, *Potonié's Lehrbuch der Paläobotanik*, 1921, p. 336; Seward, *Fossil Plants*, vol. iv. chap. xlv.; E. C. Jeffrey, *Anatomy of Woody Plants*, Chicago, 1917, chap. xxiv.; M. C. Stopes, *Catalogue of the Cretaceous Flora*, vol. ii. 1915, *passim*, esp. pp. 56-65.

The habit of the leaves of *Ginkgo* is so characteristic, that the evidence from fossil leaves, agreeing in form and venation with those of the recent genus, is in itself of some value. The evidence is in some cases strengthened by aid of the microscopic characters of the cuticle. Such leaves have been recorded in abundance, from the Coal-measures onwards, and though some are doubtful, and may probably have belonged to Ferns, resembling in their foliage *Actinopteris*, or certain species of *Schizaea*, others are beyond doubt rightly attributed to the Ginkgoales. The family appears to have attained its zenith in the Jurassic, and by the middle of that period the recent genus *Ginkgo* (if we include "*Ginkgoites*") was richly represented. Apart from *Ginkgo* itself, the genus *Baiera* of Braun is the most important group, and is distinguished from the recent plant by possessing a lamina with more numerous and narrower segments. This distinction, however, has no constant value, as some forms of leaf, even in the recent species, are much more deeply dissected than others. "The genus," says Prof. Seward, "was probably most widely spread during the Jurassic period, but there is fairly strong evidence in favour of extending its range to the Palaeozoic epoch."¹ A species, *B. Raymondi*, is known from the Permian of Autun. *B. virginiana* is also Permian, while other species are of Triassic and Rhaetic age.

The evidence from the leaves is supported by the discovery of specimens of flowers and seeds, which appear to be conclusive as to the existence of the Ginkgoales, at least in Mesozoic times. As regards the Palaeozoic evidence, Prof. Seward is of the opinion that "the plants which possessed characters nearest akin to

¹ Seward and Gowan, "The Maidenhair Tree (*Ginkgo biloba*, L.)," *Annals of Botany*, vol. xiv. March 1900. See also A. Sprecher, *Le Ginkgo biloba*, Geneva, 1907. For later accounts see Seward, *Fossil Plants*, vol. iv. 1919, chaps. xl.-xlii.; Gothan, *Potonié's Lehrbuch der Paläobotanik*, 1921, pp. 296-306.

those of *Ginkgo* were probably members of the Cordaitales, an extinct stock with which the Ginkgoaceae are closely connected."

In the Jurassic beds of Siberia, male flowers, agreeing closely with those of the recent species, have been found associated with the *Ginkgo* leaves, and similar specimens have been described from the Inferior Oolite of Yorkshire.¹ Male flowers, found in Germany at a lower horizon, on the boundary of the Trias and Lias, were associated with *Baiera* leaves, and differed from the flowers of *Ginkgo* in the greater number of pollen-sacs borne on each stamen. This point is of interest, in view of the comparison with the male flower of Cordaiteae suggested above (Chapter IV., p. 295). Female flowers and seeds have also been discovered, but as the seeds are usually detached, the evidence is not quite so satisfactory on this side.

Various genera of leaves, besides those mentioned above, have been referred, with more or less probability, to the Ginkgoales. Among these doubtful groups is the genus *Psymmophyllum*, which goes back to the Upper Devonian, if not further still. No fructification is known, and Arber gave these plants a class of their own, the Palaeophyllales.²

On the whole, the sum of the fossil evidence is of sufficient weight to prove the great antiquity of the Gymnospermous family now represented by the Maiden-hair tree, which appears to be best regarded as the one surviving member of an ancient stock, derived from the same cycle of affinity as the Palaeozoic Cordaiteae, once the dominant type of Gymnosperms.

¹ A. C. Seward, *Jurassic Flora*, Part i. 1900, p. 260.

² *Devonian Floras*, Cambridge, 1921, p. 56.

CHAPTER VI

GENERAL RESULTS

THE first broad conclusion arrived at from the study of fossil botany—the great relative antiquity of the Vascular Cryptogams and Gymnosperms, as compared with the Angiospermous Flowering Plants—still holds good, though we should now state this fundamental generalisation in rather different terms from those used by its original author, the great Brongniart.¹ The lower Seed-plants were more prominent in Palaeozoic times than Brongniart was aware, and differently constituted, for while his Asterophylliteae and Sigillarieae² have proved to be Cryptogamic families, the ranks of the Spermatophyta have received a more than equivalent accession in the Pteridosperms, now transferred to them from the Ferns. Brongniart's conclusion was far from being an obvious one at the time, for he and his contemporaries still included the Gymnosperms under Dicotyledons, so that in recognising the much higher antiquity of the former the palaeontologist anticipated the results of the comparative morphologist.

The question of the general relations and classification of the groups of plants with which we are concerned may now be best considered in connection with the early Devonian Flora.

¹ See his "Tableau des genres de végétaux fossiles," p. 93, *Dictionnaire universel d'histoire naturelle*, 1849.

² *L.c.* p. 97.

THE PSILOPHYTALES

When the earlier editions of these "Studies" were published, we had no clear knowledge of any Vascular Plants which could properly be regarded as primitive. So far, all the fossil Pteridophytes of which the structure was known, had proved to be on about the same general level of organisation as the living representatives, however much they might differ in detail. The recent work on early Devonian plants, involving the recognition of the new class Psilophytales, has changed all this, for we are now in possession of full data on the structure of certain members of an ancient race of plants, far simpler than any Vasculares known to us before. Thus we are led to look at the whole question of the relationships of the higher Classes of plants from a new point of view.

At the same time it must be borne in mind that our knowledge of the older Devonian Flora is still very limited, and, so far as structural characters are concerned, scarcely extends beyond a small and local association of peat-plants.¹ But, after making all allowances, the fact remains that the Rhynie fossils and their allies, from their age and simplicity of structure, have much the strongest claims of any known plants to be reckoned as relatively primitive Pteridophytes. This of course applies especially to the Rhyniaceae with their thalloid, Alga-like habit, without either leaves or roots, and their simple vascular system, while *Asteroxylon* already shows a definite advance (see the restorations in Figs. 135 and 136).

We have assumed that the Rhyniaceae were actually Pteridophytes, which they certainly were, if we judge

¹ On the peculiar conditions under which the Rhynie Chert was formed, see Kidston and Lang, "On Old Red Sandstone Plants showing Structure," etc., Part v., *Trans. Royal Soc. Edinburgh*, vol. lii. 1921, p. 892.

by internal structure rather than external morphology. Arber regarded the Psilophytales as much more probably

Rhynia
Gwynne-Vaughani.



FIG. 1.



FIG. 2.

Rhynia
major.

FIG. 135.—Restorations of Rhynie plants. 1. *Rhynia Gwynne-Vaughani*, showing rhizome with rhizoids, forked aerial stems with adventitious branches and dots representing the emergences, and terminal sporangia. 2. *R. major*, showing rhizome with rhizoids, naked, forked aerial stems, and large terminal sporangia. Both about half natural size. After Kidston and Lang.

Thallophytes, and he did well to emphasise their relations in this direction; his view, however, does not seriously

affect the position, for he added that *Psilophyton* (which



FIG. 136.—Restoration of Rhynie plants. 3. *Hornea Lignieri*, showing tuberous rhizome with rhizoids, forked aerial stems and terminal sporogonia. 4. *Asteroxylon Mackiei*, showing hairless rhizome, transitional region, and leafy, branched aerial stems. On the right, an associated fertile shoot, with small terminal sporangia, is shown. Both about half natural size. After Kidston and Lang.

he identified with *Rhynia*) “ while still Thallophytic in

habit may occupy anatomically a place half-way between the Thallophyta and Pteridophyta.”¹ This does not materially differ from the opinion that these plants are the most primitive of the Pteridophyta known to us.

Kidston and Lang have repeatedly called attention to the Thallophytic, and more especially Algal characters of the Rhyniaceae. Their suggestion that these plants may find their place “near the beginning of a current of change from an Alga-like type of plant to the type of the simpler Vascular Cryptogams” has already been quoted. In a later memoir they recognise the possibility that some of the Early Devonian plants may show “such combinations of characters as would break down any sharp distinction between the Algae and the simplest Pteridophytes.”² Although they do not think that this holds good for the Rhyniaceae, they point out that “the members of this class are the Pteridophyta which are most readily comparable with the Algae.”

A certain affinity with the Bryophyta has also been recognised, and it has even been held that the Rhyniaceae should be assigned to this sub-kingdom. The Sphagnum-like structure of the columellate sporangium or sporogonium of *Hornea* and *Sporogonites* may be regarded as supporting the Bryophytic attribution, which may then readily be extended to *Rhynia*. Prof. Bower has said: “Comparison of the Bryophytes will leave little doubt that the sporangium of Psilophytales and the sporogonium are kindred structures.” He adds: “The new facts are thus seen to link the Bryophytes and the Pteridophytes more closely together than before.”³ Kidston and Lang themselves point out that all three groups,

¹ E. A. N. Arber, *Devonian Floras: A Study of the Origin of Cormophyta*, Cambridge University Press, 1921, p. 49.

² Kidston and Lang, *l.c.* Part iv. 1921, p. 843.

³ F. O. Bower, *The Earliest Known Land Flora*, Royal Institution of Great Britain, April 30, 1920, p. 9.

Pteridophyta, Bryophyta, and Algae, are brought nearer together by the Rhynie fossils.

If we were to take the view that the Rhyniaceae were Bryophytes, or on the way to becoming Bryophytes, we should probably be led to regard them as in course of reduction, for their long, branched stems, though nearly or quite leafless, were far more developed than the seta of any Moss or Liverwort. The opposite theory, that they were on the up-grade, from more typical Bryophytes towards Vascular Cryptogams, scarcely seems tenable, for it would leave the admitted Alga-like features unexplained. It is wisest, however, not to carry speculation too far, and to be content with recognising that these Early Devonian plants, while themselves of the nature of very simple Pteridophytes, yet have certain points in common with the Bryophytic line. The presence of these common characters is a significant fact, whether due to affinity or to parallel development.

Dr. Church's opinion (not based on any fossil evidence) that the Land Flora sprang from highly organised Algae and that the chief features of morphological differentiation had already been acquired during marine life, has previously been cited.¹ Kidston and Lang, however, have pointed out that the absence of leaves and roots in the Rhyniaceae gives us, within the Vascular Cryptogams, a simpler starting point than this theory postulates.² As already mentioned, the existing Algae which the Rhyniaceae most nearly simulate are by no means the highest of their race. It is, however, not impossible that the modest peat-plants of the Rhynie Flora might have already undergone some reduction, a possibility hinted at above, in connection with their Bryophytic characters. However that may be, the facts clearly point to a general analogy, if not affinity, between the Rhyniaceae and fairly advanced Seaweeds. We cannot

¹ V. i. p. 421.

² Kidston and Lang, Part iv. p. 844.

go further than this, for on Dr. Church's hypothesis the transmigrant Algae belonged to some extinct group, of which we have no direct knowledge.

The uniform simplicity of the Rhyniaceae is emphasised by Kidston and Lang's conclusion that they were in all probability leafless throughout. There was at first a possibility that in *Rhynia Gwynne-Vaughani* the hemispherical emergences might represent rudimentary leaves. Recent observations have rendered this interpretation very improbable, for Kidston and Lang now find that the emergences were developed late, by the growth and division of cells of the epidermis and subjacent layers, immediately below a stoma. Thus, as they say, "it is clear that the hemispherical projections cannot be regarded as part of the primary construction of the plant as at first developed."¹ Hence "the only possible conclusion at present appears to be that the Rhyniaceae afford no clear indication as to the first origin of leaves."²

There is a considerable gap between the bare, thalloid stems of the Rhyniaceae and the leafy, Clubmoss-like shoots of *Asteroxylon*. This relatively advanced genus has been so fully discussed in Chap. X. (V. i.) that little remains to be said. *Asteroxylon*, at any rate, was an unquestionable Pteridophyte. In their later work Kidston and Lang compare it with *Thursophyton Milleri* (formerly *Lycopodites Milleri*), a Middle Devonian plant, known from impressions, looking much like a *Lycopodium*. The authors find that the similarity of *Asteroxylon* is "so great that they may be only different conditions of preservation of one species."³ There seem to be some difficulties in the way of this identification, for in species referred to *Thursophyton*, axillary sporangia, totally different from the fructification attributed to *Asteroxylon*, have been described.⁴ In any case, however,

¹ Kidston and Lang, Part iv. p. 833.

² *L.c.* p. 848.

³ *L.c.* p. 852.

⁴ See Arber, *Devonian Floras*, p. 29.

the similarity in the vegetative habit of the two genera is striking.

Asteroxylon, if it were not for the peculiar fertile shoots associated with it, might be regarded as an early representative, or at least precursor, of the Lycopod series, resembling the Psilotales in the absence of differentiated roots. If we accept the fertile shoots as belonging to the plant (which seems very probable from the close association) we get the extraordinary combination of characters already discussed in Vol. I. Until certainty is attained on this point, it is useless to carry the discussion further.

The most fundamental question concerning the affinities of the Vascular Plants is whether their several phyla diverged from a common stock, already vascular, or ran back in distinct parallel lines to different ancestral races among the Algae. Unfortunately the question is insoluble, and both views are maintained by competent authorities. Attention has already been called to the extreme polyphyletic theory of Dr. Church, and to the monophyletic origin suggested by Dr. Halle.¹ The former holds that "all the main lines of what is now Land Flora must have been differentiated in the Benthic Epoch of the sea (*i.e.* as algal lines)." ² Dr. Halle, after pointing out the possible relation of the *Psilophyton* type to both Lycopods and Ferns, remarks that "from this point of view the whole pteridophytic stock would be monophyletic, the Lycopsida and Pteropsida being derived from a common form already vascular."

Kidston and Lang accept Halle's conclusion as "a fair statement of the present bearing of the imperfectly known facts." While they hold that the type of the Rhyniaceae "suggests the convergence of Pteridophyta and Bryophyta backwards to an Algal stock," they

¹ V. i. pp. 416 and 421.

² A. H. Church, "Thalassiophyta and the Sub-aerial Transmigration," *Botanical Memoirs*, No. 3, Oxford, 1919, p. 41.

add: "The knowledge of *Asteroxylon* confirms and enriches our conception of a more complex but archaic type of the Vascular Cryptogams which supports the idea of the divergence of the great classes of Pteridophyta from a common type and links this on to the Rhyniaceae."¹ In a later memoir they express the further opinion that "it is perhaps better to regard the point of divergence as represented by plants somewhat simpler than the Asteroxylaceae in that they did not possess definite small leaves."²

On the other hand, Dr. Arber, like Dr. Church, but from a quite different point of view, maintained a polyphyletic evolution of the higher plants. He recognised three distinct main lines of descent, the Sphenopsida, Pteropsida, and Lycopsida, descended severally from Thallophytic Algae of different types. He regarded it, however, "as probable that the Psilophyton habit was primitive for all three lines of Cormophytic descent."³ He derived the Sphenopsida "from Thallophytic Algae bearing whorled branches," of limited growth and "typically small, converted into leaves which were originally and always microphyllous." The Pteropsida were "descended from Thallophytic Algae in which the branches were large, numerous, scattered and not whorled." The compound branches were "eventually metamorphosed to megaphyllous leaves." On the other hand, Arber derived the Lycopsida from Algae "in which the aerial axes were rarely branched and then usually in a dichotomous manner. The branches bore emergences, which were metamorphosed to microphyllous leaves."⁴

Arber separated the Psilotales altogether from the Palaeozoic lines, making them "a quite independent

¹ Kidston and Lang, Part iii. p. 675.

² Kidston and Lang, Part iv. p. 843.

³ E. A. N. Arber, *Devonian Floras*, p. 72.

⁴ Arber thus adopted Lignier's distinction between true leaves, modified from thalloid branches, and phylloids, derived from emergences.

race, also of Algal origin, which appeared on the scene long after the other races—possibly in Mesozoic times, or even later.”¹

On the whole the recent trend of botanical speculation has perhaps been in a polyphyletic direction. At the same time it must be admitted that the discovery of the existence, in Early Devonian times, of an excessively simple race of Vascular Plants may turn the scale in favour of a common origin from a vascular stock. The important characters common to all existing Pteridophyta, however diverse, have always supported the idea of a single origin. Among such characters the chief are : the alternation of generations with the sporophyte predominant ; the development both of the asexual and the sexual reproductive organs, and the histology, as shown especially in the vascular tissues and the stomata. So far as the evidence shows, these common characters probably extended to the fossil groups also. Such arguments, however, are far from conclusive, for the community in reproductive phenomena may be explained, with Dr. Church, on the principle that such phases are inevitably passed through, and must therefore be the same in all phyla. In like manner some of the common somatic features may be the necessary consequence of the sub-aerial transmigration.

In framing a provisional classification of the great groups of Vascular Plants we must therefore realise that the relations between them are still wholly hypothetical. With this reservation we may adopt the following scheme, modified from that given in the second edition of this book, but as far as possible following the same general lines.

PSILOPHYTALES	{ Rhyniaceae Asteroxylaceae
LYCOPSIDA	{ Psilotales (?) Lycopodiales

¹ Arber, *l.c.* p. 87.

SPHENOPSIDA .	$\left\{ \begin{array}{l} \text{Equisetales} \\ \text{Pseudoborniales} \\ \text{Sphenophyllales} \end{array} \right\}$	<i>Articulatae.</i>
PTEROPSIDA .	$\left\{ \begin{array}{l} \text{Filicales} \\ \text{Pteridospermeae} \\ \text{Gymnospermeae} \\ \text{Angiospermeae} \end{array} \right\}$	<i>Spermophyta.</i>

The position provisionally assigned to the Psilotales in this scheme requires a word of explanation. I now regard their affinities as entirely uncertain. We are not directly concerned with them in these "Studies," for no fossil representatives are known. In previous editions, however, great stress was laid on the apparent affinity of this recent family with the Palaeozoic Sphenophyllales. In the second edition the evidence was given in some detail, and the Psilotales were definitely included under the Sphenopsida. Since that time our knowledge of this recent group has been greatly enriched owing to the discovery and investigation of the prothallus and embryo by Darnell-Smith, Lawson, and Holloway.¹ Prof. Lawson expresses himself favourably towards the affinity with Sphenophyllales, while pointing out that the gametophyte generation can offer no positive evidence. Dr. Holloway in his later paper says: "The extreme simplicity of the *Tmesipteris* embryo, wholly devoid as this is of appendicular organs, is full of significance, and the demonstration of a rootless and leafless condition in the earliest known land-plants strengthens the belief that the Psilotaceae have preserved in the first stages of their development primitive features."² Thus he supports, in a general way, the views of Kidston and Lang.

¹ A. A. Lawson, "The Prothallus of *Tmesipteris tannensis*," *Trans. Royal Soc. Edinburgh*, vol. li. 1917; G. P. Darnell-Smith, "The Gametophyte of *Psilotum*," *ibid.* vol. lii. 1917; A. A. Lawson, "The Gametophyte Generation of the Psilotaceae," *ibid.* vol. lii. 1917; J. E. Holloway, "The Prothallus and Young Plant of *Tmesipteris*," *Trans. New Zealand Institute*, vol. l. 1918; "Further Studies on the Prothallus, Embryo and Young Sporophyte of *Tmesipteris*," *ibid.* vol. liii. 1921.

² Holloway, *l.c.* 1921, p. 421.

Hence there are four theories in the field as to the position of this problematic group :

1. That of Kidston and Lang, now supported by Holloway and Bower,¹ that the Psilotales are nearest to the Devonian Psilophytales.
2. Arber's suggestion that they are of late and independent origin from Algae.
3. The hypothesis maintained by A. P. W. Thomas, and formerly by Bower and myself, of an affinity with the Sphenophyllales.
4. The old-fashioned view that the Psilotales are essentially Lycopods.

On present evidence it seems probable that the Psilotales may have retained some primitive characters, notably the negative one of the absence of roots ; as no root appears in the embryo of *Tmesipteris*, we may suppose that this is an original deficiency. On the other hand, any near affinity to the Psilophytales seems to the present writer improbable—*Psilotum* has obviously undergone reduction, and *Tmesipteris* appears to bear no resemblance in external morphology to any of the Early Devonian plants. The synangia are evidently advanced and specialised organs ; the anatomy, however, shows a considerable likeness to that of *Asteroxylon* on the one hand, and certain Lycopods on the other. It is perhaps safest at present to return to the old idea of a certain relationship to the latter class, while such primitive features as are present in the Psilotales may be recognised by putting them near the Psilophytales, though within the Lycopsidea. It seems more probable that they are aberrant Lycopsidea than that they were directly derived from the remote Devonian group.

The theory once held that the Psilotales are nearest to the Sphenophylls must, it seems, be dropped. There are no doubt some remarkable analogies, especially in the morphology of the synangia, but these may well

¹ " The Earliest Known Land Flora," *R.I.* 1920, p. 6.

be only homoplastic. The whorled phyllotaxis is so constant throughout the recognised Sphenopsida that it should probably be accepted as an essential character of the Division. The remarkable variations in the sporophylls of *Tmesipteris*, observed by A. P. W. Thomas,¹ retain their interest, but have perhaps been over-estimated as indications of affinity.² The analogy of some of his peculiar forms, with *Sphenophyllum majus*, on which stress was formerly laid by the present writer, proves to be less close than it then appeared (see V. i. p. 101).

Thus the affinities of the Psilotales remain quite an open question; the position now assigned to them in our scheme is merely intended to indicate a tenable suggestion.

With reference to the scheme given on p. 395, it must be pointed out that, while our old Division Pteropsida is retained, the Spermatophyta are now regarded as an independent phylum, not descended from the Filicales, though very probably derived ultimately from a common source with them.

LYCOPSIDA

The points of agreement, both external and structural, between the ancient genus *Asteroxylon* and some of the Lycopods have already been pointed out in Chap. X. (V. i.). Several of the Early Devonian plants had a more or less Clubmoss-like habit, and it seems not improbable that a real affinity may exist between the Lycopodiales and some of the Psilophytales. Thus there is now a possible clue to the early history of the Lycopod phylum.

The dubious position of the Psilotales, which we have placed provisionally under the Lycopsida, has been sufficiently discussed above.

¹ A. P. W. Thomas, "The Affinity of *Tmesipteris* with the Sphenophyllales," *Proc. Royal Society of London*, vol. lxi. 1902, p. 343.

² Cf. Holloway, *l.c.* 1921, p. 417.

In the first edition of these "Studies" I laid stress on the relation of the Lycopods to the Sphenophyllales, and, through them, to the Equisetales. Prof. Jeffrey, on independent grounds, united all these classes in his Lycopsida,¹ as a main division of Vascular Plants, while his Pteropsida included all the remaining groups. It now appears probable that the Articulatae were derived from relatively megaphyllous plants, whereas we have at present no evidence that the Lycopods were ever anything but microphyllous, like their predecessors among the Psilophytales. Further, the Articulatae are "sporangio-phoric," bearing their sporangia on special appendages, whereas throughout the Lycopods we find a single sporangium seated directly on the sporophyll, or in its axil. This simple arrangement may also be due to reduction; the ventral outgrowth of the sporophyll which bears the sporangium in *Spencerites* has been compared to the sporangio-phore of Sphenophyllales, and Dr. Benson has interpreted the sterile tissue of the sporangium in *Mazocarpon* as representing a sporangio-phore. These suggestions are very interesting, but at present too hypothetical for any conclusion as to affinity to be based on them² (see below, p. 407).

In the anatomy there is no doubt a considerable analogy between the Lycopods, especially the Palaeozoic types, and the Sphenophyllales. The stelar structure of *Cheirostrobus*, for example, is much like that of a *Lepidodendron* such as *L. selaginoides*, allowing for the fact that the leaf-arrangement is verticillate in the one and spiral in the other. This type of stele,³ however,

¹ E. C. Jeffrey, "Structure and Development of the Stem in the Pteridophyta and Gymnosperms," *Phil. Trans. Royal Soc. B*, vol. 195, 1902, p. 144; also his earlier papers there cited. See also his later work, *The Anatomy of Woody Plants*, Chicago, 1917, chap. xviii.

² See also Miss M. G. Sykes (Mrs. Thoday), "Notes on the Morphology of the Sporangium-bearing Organs of the Lycopodiaceae," *New Phytologist*, vol. vii. 1908, p. 41. The views of Kidston and Lang are given in their fourth memoir on *Old Red Sandstone Plants*, etc., p. 849, 1921.

³ *I.e.* an exarch protostele.

may also occur in Ferns (though not characteristic of that class) ; its wide distribution is one of the facts in favour of an ultimate common origin for all the vascular phyla (see above, p. 393).

The Lycopods manifestly attained their highest development in later Palaeozoic times as regards abundance, stature, and organisation, both vegetative and reproductive. In spite of their immense development at that time compared with their very subordinate position at the present day, the Lycopods, as a whole, constitute a very homogeneous class of plants, characterised throughout by a microphyllous habit, an anatomy based on an exarch type of protostele (sometimes slightly mesarch), and a simple relation between sporangium and sporophyll. There is no departure from the first-named character ; for though the leaves were often long, they were never large in proportion to the plant, and were always of the simplest form. The double bundle of *Sigillariopsis*, a form of leaf belonging to certain species of the somewhat advanced genus *Sigillaria*, is the only departure from the prevailing simple type of foliar structure (V. i. p. 207).

Attention has already (V. i. 112) been called to the simplicity of the primary anatomical structure of the stem in Palaeozoic Lycopods, the one character in which these plants have proved to be more " primitive " than most of their recent allies. A gradual transition may be traced from the protostelic type, through the medullated forms of *Lepidodendron* and the ribbed *Sigillarias*, to the smooth-barked *Sigillarias*, in which the ring of wood separates, more or less completely, into distinct bundles (V. i. 198). It is these last forms which depart most widely from the common Lycopod type, but the change is not a great one, and does not appear to indicate a transition to any form of Gymnospermous stem.

As regards the secondary growth, characteristic of the arborescent *Lepidodendreae*, there are some peculiarities ;

the agreement with the normal secondary thickening of Gymnosperms and Dicotyledons is somewhat less exact in this class than in the Sphenopsida or the Pteridosperms. In some forms (*Lepidophloios fuliginosus*, for example, V. i. 137) the zone of thickening is extremely irregular, and although in other *Lepidodendreae* it approaches the normal type more nearly, it is doubtful whether in any case the same cambium remained continuously active throughout. The secondary growth of *Isoëtes* presents some interesting analogies with that of the *Lepidodendreae*.

The enormous development of the secondary cortical tissue, chiefly phelloderm, is a striking feature of the tree Lycopods, and with this again the growth of the cortex in *Isoëtes* alone presents any analogy, though, at best, only a remote one.

The difficult question of the morphology of *Stigmaria*, the subterranean part of the *Lepidodendroid* plant, already discussed (V. i. 236), suggests that the differentiation between "root and shoot" may have been less sharp in this group than in other Vasculares. Similar indications are to be found in the rhizophores of *Selaginella* and the stem-like roots of some *Lycopodiums* at the present day. The absence of true roots in the Psilophytales is significant in this connection. A suggestion has been made by Prof. F. E. Weiss that an analogy for the Stigmarian axes may be found in the protocorm, the rudimentary, somewhat thalloid, stem which is the first product of germination in some species of *Lycopodium*, and appears to be persistent in the tuber of *Phylloglossum*. In *Hornea*, among the Psilophytales of the Devonian, the rhizome was of the nature of a protocorm (see V. i. 388).

It is a curious fact that among the very numerous fructifications that have been investigated, no certain instance of a homosporous Palaeozoic Lycopod has yet been discovered. Wherever the material has allowed of

a definite conclusion, two forms of spore, as sharply differentiated as in any recent members of the class, have been found. *Spencerites* is sometimes cited as an exception, but the evidence is inconclusive, and the spores are singularly unlike those of any known homosporous Lycopod (V. i. 170). The oldest known genus of Lycopods, *Bothrodendron*, was markedly heterosporous, as shown both in the Upper Devonian and the Coal-measure species. Among the herbaceous as well as the arborescent Lycopods, only heterosporous forms have so far been detected; in some of the former (*Selaginellites primaevus*) there is an exact agreement with the recent *Selaginella* (V. i. 241).

It must, however, be remembered that heterospory is always easier to demonstrate than homospory. It is impossible to doubt that homosporous Lycopods existed in Palaeozoic times, but the prevalence of higher methods of reproduction shows how far the class had already advanced at the period when the fossil record of indubitable Lycopodiales begins.

Certain Carboniferous Lycopods, as we have seen (V. i. 173), went beyond mere heterospory, and developed organs closely analogous to true seeds. Of the two genera in which seed-like organs are known, the one, *Lepidocarpon*, clearly belonged to the Lepidodendreae, while the other, *Miadesmia*, appears to have been a small herbaceous plant, perhaps, as Dr. Benson has suggested, epiphytic on the larger Lycopods with which it is associated. The affinities of *Miadesmia*, which in some respects resembles a *Selaginella*, are not yet determined, but in any case it seems clear that this genus acquired the seed habit on its own lines, and independently of *Lepidocarpon*. The single-spored units formed on the fragmentation of the megasporangium of *Mazocarpon* offer a certain analogy with seeds.

The seed-like organs of *Miadesmia* and *Lepidocarpon*, though they may probably have been functionally seeds

in the same sense as those of the Pteridosperms, are greatly inferior to the latter in morphological differentiation, and stand much nearer the Cryptogamic type of megasporangium. They are, in fact, the only really "primitive" seeds known to us, and as such are of special interest, though they probably only represent a sideline of evolution.

As regards the relation of the Palaeozoic to the recent Lycopods, only the heterosporous forms of the latter come under consideration, for as yet we know nothing certain of the history of the homosporous Lycopodiaceae, apart from the possible relation to the Psilophytales. It now seems clear that the genus *Selaginella*, or types scarcely distinguishable from it, already existed in the later Palaeozoic Flora, and that it had no near relation to the arborescent Lepidodendreae. On the other hand, there may well be some connection between the Lepidodendreae and the greatly reduced heterosporous genus *Isoëtes*, which, in the structure and insertion of its sporangia, as well as in anatomical characters, has much in common with the Palaeozoic tree Lycopods. In the occurrence of sterile trabeculae in the sporangia of some *Lepidostrobi*, Prof. Bower has recognised an interesting point of agreement with *Isoëtes*.¹

The question of a possible relationship between the Palaeozoic Lycopods and certain Seed-plants will be discussed when we come to the Gymnosperms.

¹ The curious Triassic genus *Pleuromeia* has been regarded as a link between the two groups, but if, as is stated, the sporangia of *Pleuromeia* were borne on the underside of the sporophyll, there is great difficulty in accepting this view. On *Pleuromeia* see Solms-Laubach, "Über das Genus *Pleuromeia*," *Bot. Zeitung*, Bd. lvii. 1899, p. 227; H. Fitting, "Sporen im Buntsandstein—die Makrosporen von *Pleuromeia*?" *Ber. d. Deutschen Bot. Gesellschaft*, Bd. xxv. 1907, p. 434. For a possible solution of the difficulty see Dr. M. Benson, "*Mazocarpon*, or the structure of *Sigillariostrobus*," *Ann. of Bot.* vol. xxxii. 1918, p. 586.

SPHENOPSIDA

The general morphological agreement between the two classes Sphenophyllales and Equisetales is manifest, and extends to Nathorst's class Pseudoborniales. The articulated stem, and the constant verticillate arrangement of the appendages, are characters obviously common to the whole series. *Archaeocalamites*, the oldest of the known Equisetales, distinctly approaches the Sphenophyllales in the superposition of the verticils and in the dichotomously divided leaves, while in many Calamariaceae the individual leaves resemble the leaves or leaf-segments of the plurifoliate Sphenophyllums so closely as to be almost indistinguishable. Lignier endeavoured to carry the comparison further and to place it on an anatomical basis. In the species of *Sphenophyllum*, regarded as typical, there are six leaves in a whorl, but the vascular strands supplying each two leaves start from the same angle of the triarch stele, suggesting that three was the original number of leaves in a verticil, a supposition for which there is no palaeontological evidence. In some species (e.g. *Sphenophyllum Dawsoni*, V. i. 90) the stele itself is hexarch, each of its angles being double. When the leaves are further segmented, a further forking of the bundles takes place within the cortex, and it might be supposed that the numerous leaves of such a species as *S. myriophyllum* represent the segments of a few deeply divided original appendages. As a matter of fact, however, the oldest known species of *Sphenophyllum* (e.g. *S. subtenerrium* from the Upper Devonian) have numerous leaves, narrow and forked, in a whorl. In the Calamariaceae, on Lignier's view, the supposed process had gone further, the increased dimensions of the stem involving a corresponding multiplication of the leaves and of the bundles in the stem. In cases like the axis of *Calamostachys*, we may find an analogy with *Sphenophyllum* in the fact that each two bracts receive their

vascular supply from the same axial bundle, while in *Palaeostachya vera* the axial bundles are themselves duplicated, forming evident pairs (V. i. 57). While Lignier's theory is not supported in detail by the fossil evidence, a clear analogy between the Sphenophylls and the Calamariaceae can be traced. That the leaves of the Sphenopsida were originally compound or much cut is suggested by the presence of such divided leaves in the early fossils *Archaeocalamites*, and more especially *Pseudobornia*, the leaves of which, when found isolated, were actually taken for the fronds of a Fern.

In anatomy, the Sphenophyllales, with their solid protostele, appear to be clearly more primitive than the Equisetales, which in all cases have a pith and distinct vascular bundles. The anatomical gap between the two classes appeared a very wide one, until it was partly bridged by the discovery of centripetal wood in the stem of the Lower Carboniferous *Protocalamites* (V. i. 32).

The evidence from the fructifications strongly supports the affinity between Sphenophyllales and Equisetales, though the detailed comparison presents some difficulties. The minute structure of the sporangia is strikingly similar in the two classes, and the resemblance extends to the sporangiophores. Those of *Cheirostrobus* in particular, which have four sporangia, are almost identical with those of *Calamostachys* (V. i. 48, 103). Where the number of sporangia is smaller the resemblance to the Equisetal type becomes less evident.

The question of the nature of the sporangiophore has been profoundly affected as we shall see by recent work on the Early Devonian plants. We may first recapitulate the facts.

Throughout the Sphenophyllales the sporangiophores occupy the position of ventral lobes of the sporophyll; in one species, *S. fertile* (V. i. 100), the dorsal lobes are also enlisted for the same service. This latter case is of special interest, because the dorsal and ventral lobes

are on an equal footing, both being organised in the same way; the segments of each lobe constitute typical bisporangiate sporangiophores. I incline to regard this form as a secondary modification rather than a primitive type, partly because the case is at present altogether exceptional and of no special antiquity, and partly because the dorsiventral arrangement seems best explained on the supposition that the dorsal lobes were originally sterile and protective in function. It may be added that the very leaf-like character of the bracts in most *Sphenophylls*, and especially in *Sph. majus* (V. i. 101), makes it difficult to explain them as sterilised sporangiophores. But whether we regard *S. fertile* as a modified or a primitive form,¹ it may be interpreted as showing that the sporangiophores and bracts have equal claims to be regarded as lobes of the sporophyll. Or we may, with Dr. Margaret Benson, call the sporophyll here "a leaf wholly composed of sporangiophores." The ventral position holds good also for *Cheirostrobus*; it is only in *Sphenophyllum emarginatum* that the sporangiophores and bracts appear to have been independent, as they have left separate scars on the axis of the cone.²

In *Calamostachys*, among the Equisetales, the two organs are externally quite separate, but the course of the bundles supplying the sporangiophores suggests that the latter may represent displaced ventral appendages of the bracts (V. i. 53). *Palaeostachya*, from the position of the sporangiophores immediately above the bracts (V. i. 58), seemed at first to form a link with the Sphenophyllales, but Dr. Hickling's observations on the vascular supply rather suggest a modification of the *Calamostachys* arrangement. The *Equisetum* type of strobilus appears to have been already represented in Palaeozoic times,

¹ The latter view was maintained by Lady Isabel Browne in her interesting résumé of the "Phylogeny and Inter-relationships of the Pteridophyta," *New Phytologist*, vol. vii. 1908, p. 94.

² As shown by unpublished observations of Mr. W. Hemingway's.

and in *Archaeocalamites* the bract-whorls were, at most, few and scattered. It has been proposed to derive the bractless arrangement from that found in *Sphenophyllum fertile*, the assumption being that the lobes of a wholly fertile sporophyll underwent a displacement like that which appears to have taken place between the sterile and fertile lobes in *Calamostachys*.¹ The evidence, however, is as yet insufficient to establish any such interpretation, and it may well be that the *Sphenophyllum* analogy has been pushed too far. There is no need to reduce every sporangiophore to a leaf-lobe, for it is possible to hold that in the Sphenopsida, as in the Pteropsida, the spore-bearing organ may be sometimes a lobe of a leaf, sometimes an entire leaf, or not of foliar nature at all.

Prof. Bower regarded the sporangiophore as "a part *sui generis* as much as the sporangium is, and not the result of modification of any other part."² We now have good reason, from the evidence furnished by the Rhyniaceae, for believing that the sporangium itself is *not* an organ *sui generis*, but the modified end of a branch.³ Hence it seems natural to suppose that the sporangium-bearing organ, the sporangiophore, represents a fertile branch of the early Pteridophytic thallus. Dr. Margaret Benson, in 1908, anticipated this suggestion, saying, "With the new hypothesis [Prof. Lignier's] in view, such organs may be explained as units of the Pteridophytic thallus which still exist as relics of the condition in which the limits of axis and leaf were not fixed."⁴ Kidston and Lang, writing in the light of their Rhynie discoveries, say: "The sporangiophores would appear to represent the last persisting remains of the original leafless branch-

¹ Scott, "Present Position of Palaeozoic Botany," *Progressus Rei Botanicae*, Bd. i. p. 162, 1906.

² *Origin of a Land Flora*, p. 426.

³ See V. i. 394.

⁴ M. Benson, "The Sporangiophore, a Unit of Construction in the Pteridophyta," *New Phytologist*, vol. vii. 1908, p. 148.

systems of the Rhyniaceae.”¹ They apply this comparison to the sporangiophores of the Equisetales and Sphenophyllales, with which we are here concerned, as well as to those of *Helminthostachys*, the fertile appendages of the Psilotaceae, and “with greater difficulty and obscurity to the position of the sporangia of the Lycopodiales.”

Thus the cauline theory of the sporangiophore is confirmed, but with a difference; we need not regard this organ as belonging to the category “axis” as distinguished from “leaf”; it represents the branch of a thallus and belongs to a phase before leaf and axis were differentiated.² It seems quite probable that this interpretation may hold good for many cases; it must, however, be remembered that the leaf is also, on the view now held, a modified branch of a thallus. It is possible that sometimes the leaf may have preceded the specialised sporangiophore in its differentiation. Thus, if, as we have suggested, the fertility of both dorsal and ventral segments in *Sphenophyllum fertile* is a secondary and not a primitive character, it is probable that the dorsal part was a leaf before it became converted into sporangiophores.

However this may be, there is no doubt that our present knowledge of the simple morphology of the Rhyniaceae greatly illuminates the question of the sporangiophore, and brings into harmony various divergent views previously maintained. The independent sporangiophores of the *Archaeocalamites* type³ may quite

¹ Kidston and Lang, Part iv. p. 850.

² Cf. M. G. Sykes (Mrs. Thoday), “Anatomy and Morphology of *Trisopteris*,” *Ann. of Bot.* vol. xxii. 1908, especially p. 82.

³ On the sporangiophores of the *Equisetum* type, see Lady Isabel Browne, “Anatomy of the Cone and Fertile Stem of *Equisetum*,” *Ann. of Bot.* vol. xxvi. 1912, vol. xxix. 1915, vol. xxxiv. 1920, vol. xxxv. 1921. Also Kate Barratt, ‘A Contribution to our Knowledge of the Vascular System of the Genus *Equisetum*,’ *Ann. of Bot.* vol. xxxiv. 1920.

well be interpreted as derived directly from fertile thallus-branches ; in other cases the association between sporangiophore and leaf has become so close that it is impossible to say which was the first to be differentiated.

The genus *Sphenophyllum*, as we have seen, goes back to the Upper Devonian. Very little is known of the earlier history of the Articulatae, but Nathorst has described a plant (*Hycnia sphenophylloides*) from West Norway, probably of Middle Devonian age, which seems to have been a precursor of *Sphenophyllum*. The fossil only differs from that genus in the absence of definite nodal lines, and perhaps in the number of leaves in a whorl, which was more probably four than six. Nothing is known of the fructification.¹ This seems to be the earliest authentic geological record for the Sphenopsida.

On the whole of the evidence there can be no doubt that a real affinity exists between the Sphenophyllales and the Equisetales, the former being clearly the more primitive class of the two, or rather the representatives of a more primitive stock, for the known Sphenophylls are evidently specialised in various directions. The arguments for the aquatic habit of *Sphenophyllum* do not hold good, as already pointed out (V. i. 77) ; the great development of the wood relatively to the size of the stem is the reverse of what one would expect in a water-plant ; on the other hand, Prof. Seward's suggestion that *Sphenophyllum* may have been " a slender plant which flung itself on the branches and stems of stronger forest trees for support," ² agrees well with the habit and structure. The occurrence of extensive secondary growth in this genus is interesting, as showing that this character was not necessarily correlated, even in Palaeozoic times, with an arborescent habit.

¹ A. G. Nathorst, "Zür Devonflora des westlichen Norwegens," *Bergens Museums Aarbok*, 1914-15, No. 9. See also Arber, *Devonian Floras*, p. 53.

² *Fossil Plants*, vol. i. 1898, p. 392.

The enormous development of the Equisetales in early geological periods, compared with their reduced condition at the present day, is a striking fact. It is of interest to consider in what respects the gigantic Palaeozoic Horsetails differed from their humbler successors.

One great and obvious difference was the formation of secondary wood and bast and of periderm. Starting with a structure in stem and root essentially like that of a recent *Equisetum*, the Calamariaceae, by the activity of a normal cambium, produced new wood and phloem, to an indefinite extent, precisely as in a Gymnospermous tree, and replaced their primary cortex by a broad zone of secondary periderm. It was one of Williamson's greatest services to science that he always, in the face of much opposition, insisted on the true "exogenous growth" of the Calamites, while maintaining with equal decision their Cryptogamic nature. He thus established one of the most striking instances of homoplastic modification, for the close agreement in these anatomical characters between certain Cryptogams and Phanerogams is not, in itself, any proof of affinity.

As has already been pointed out, it is probable that the microphyllous character is not a primitive one in Equisetales, and that the leaves are reduced from a larger and more complex type, as seen in *Archaeocalamites* and *Pseudobornia*. Although Arber spoke of the Sphenopsida as "microphyllous" he recognised a sharp distinction between their leaves and those of the Lycopsidea.

The old opinion of the French school, that some Calamariaceae were seed-bearing plants, has not been substantiated by later work. Heterospory, however, appears in a perfectly well-marked form in some of the fructifications, though the differentiation of the two kinds of spore was not so extreme as in heterosporous Lycopods or the recent Water-ferns. In other Calamarian strobili the evidence is all in favour of homosporous; the abortion of certain spores in sporangia of this type may have

prepared the way for the heterospory of the more advanced members of the group (V. i. 49). In this respect the Equisetales seem to have reached a higher level than the Sphenophyllales, among which only doubtful indications of incipient heterospory have so far been detected. The Pseudoborniales, however, are described as heterosporous.

Considering the high development of the Palaeozoic Equisetales, it is an interesting question whether our living Equiseta are their degenerate descendants, or the offspring of a simpler stock which may have co-existed with the arborescent forms in ancient times. The earlier Mesozoic Equisetales appear to have been intermediate in certain respects between the Calamariaceae and the recent genus, as shown especially by Prof. Halle's results (V. i. 72). By Wealden times, forms almost identical with modern Horsetails had appeared. These facts favour the hypothesis of reduction, though, as in all such questions, we cannot hope to trace direct descent. The Equisetales, as a class, have conspicuously failed to hold their own in the secular struggle for existence, though the survivors are extraordinarily well adapted to particular conditions, and maintain their ground, when once established, with singular obstinacy.

PTEROPSIDA

Filicales.—The result of the palaeobotanical research of the last twenty years has been to exalt the importance of the Fern phylum, on account of its remarkable parallelism with the Pteridosperms, probably the source from which a large part, if not the whole, of the Seed-plants was derived. At the same time the recent discoveries have greatly reduced our estimate of the actual number of the true Ferns in Palaeozoic times (most of the so-called Ferns having been Seed-plants at that period), and difficulties have arisen in discriminating between the Ferns proper and the Pteridosperms. Among indubitable

Palaeozoic Filices we have, in the first place, the Order Botryopteridaceae and a few other forms probably allied to them. We may follow the late Dr. Arber¹ in using the name Primofilices for the whole group. As regards the Marattiaceae, long considered as the dominant Ferns of the Carboniferous period and really an important group, the question is in some respects more difficult, as has been shown in Chapter VIII. (V. i.).

There is no reasonable doubt that the Botryopteridaceae were true Ferns; all their characters, both vegetative and reproductive, point in this direction, and the evidence has been materially strengthened by the observation of spores in process of germination, agreeing closely with corresponding early stages in the development of recent Fern prothalli (V. i. 333).

Anatomically, the Botryopteridaceae show two types of structure, the one (Botryopterideae, V. i. 337) exceedingly simple as regards the stem-structure, while the other (Zygopterideae, V. i. 288) shows a considerable degree of differentiation. The solid strand of tracheides, surrounded by phloem, which constitutes the central cylinder in the *Botryopteris* group, is perhaps the simplest form of stele known in any Fern, but it would be rash to infer from this fact that these plants were necessarily of a specially primitive nature. Their roots are diarch, like those of most recent Ferns, their petioles attain some degree of complexity in vascular structure, while the differentiation of special fertile fronds, for which there is here some evidence, may indicate a rather high grade of organisation.

The affinities of the Botryopteridaceae with other Ferns have been fully discussed in Chapter IX. (V. i.), and the conclusion arrived at, that while they show some analogy with various Filicinean families of later origin, they cannot be considered as on the direct line of their descent.

¹ E. A. N. Arber, "On the Past History of the Ferns," *Ann. of Bot.* vol. xx. 1906, p. 221.

This line will have to be sought among other Primofilices, of which, as yet, we have only a scanty knowledge, though the occurrence of annulate sporangia on ordinary Fern pinnules, as in *Pteridotheca Williamsonii*, is a promising indication (V. i. 265).

Some relation between the Botryopteridaceae and the Ophioglossaceae was recognised by Renault when he first discovered the fossil family, the resemblances he detected lying in the fructification and in the occurrence of reticulated tracheides. He regarded the Botryopteridaceae as intermediate in stem and fructification between the Hymenophyllaceae, representing the Ferns properly so-called, and the distinct group Ophioglossaceae.¹ These relations have been discussed in Chapter IX. (V. i.). The sporangia of *Stauropteris* (a genus not known to Renault) present an almost exact agreement with those of *Botrychium*, as regards their structure and the mode of attachment by vascular pedicels.² It may be recalled that the structure of the stem in the Zygopteridean genus *Botrychioxylon* (V. i. 319) if it lost the internal wood (a change likely to occur, from the analogy of parallel cases elsewhere³) would be almost exactly that of *Botrychium*, in which medullary tracheides sometimes occur. The fact that the frond (at least the fertile frond) of many Zygopterids branched in more than one plane has been compared with the dorsiventral branching of the frond characteristic of Ophioglossaceae.⁴

On the whole, a real if somewhat remote affinity between the fossil and the recent family seems probable—in fact, of known plants, it is the Botryopteridaceae which appear to have most in common with the Ophioglossaceae.

¹ B. Renault, *Végétaux silicifiés d'Autun*, etc., Autun, 1878, p. 114.

² In *Botrychium* they are short, in this respect resembling those of *Botryopteris*.

³ See below, p. 421.

⁴ Lady Isabel Browne, "Phylogeny and Inter-relationships of Pteridophyta, vi. Filicales," *New Phytologist*, vol. vii. 1909, p. 27.

A relation between the Botryopteridaceae and the Osmundaceae has been clearly established, especially by the anatomical investigations of Kidston and Gwynne-Vaughan (see V. i. 362).

Prof. Kubart's discovery of the fructification of *Anachoropteris* (V. i. 354) shows that plants included under Botryopteridaceae had developed complex synangia, comparable to those of advanced Marattiaceae. The agreement in this respect is so close, as to suggest an affinity between the two groups. But this is no more than a suggestion. There can be no reasonable doubt that the Marattiaceae or allied Ferns formed a considerable element in the Upper Carboniferous Flora (Chapter VIII., V. i.), but we know nothing of their history in earlier periods.

True Ferns (*e.g.* *Archaeopteris*) appear to have been well developed in the Upper Devonian times; at least there is no sufficient reason for assuming that the fern-like plants of that age were all Pteridosperms. When we go back to the Early Devonian, the case is quite altered, for, as we have already seen, the evidence seems to indicate that the so-called Ferns of those days did not possess a lamina, but bore fronds of the nature of a naked, branched rachis (V. i. 415). Such "fronds" are scarcely to be distinguished from the ramifications of a thalloid stem. Thus the available facts suggest that in the older Devonian Flora, Ferns, as such, may not yet have existed, though of course their precursors (such as Lignier called *Primofilicinées*) were present. Possibly we may have, in plants such as *Stauropteris*, a Carboniferous race which had retained the naked rachis while in other respects attaining the grade of Ferns (see V. i. 335, 413).

Spermophyta.—While we have no proof of the existence of true Ferns in the Early Devonian period, there is good evidence for the presence of highly organised Pteridospermous or Gymnospermous stems (*e.g.* *Palaeopitys*

Milleri) in the Middle Devonian. This subject is now under further investigation, but the existing data, such as they are, support the opinion that the Seed-plants cannot have been derived from Ferns, properly so called, for the line of the Spermatophyta seems to go back as far as, or even farther than, that of the Ferns themselves.

The resemblances which have been traced between the Marattiaceae and the Pteridosperms, especially between the sporangia of the former and the pollen-sacs of the latter, are not likely to be due to descent of the Spermatophytic from the Cryptogamic group, for, so far as we know, the Pteridosperms are considerably older than the Marattiaceae. Dr. Kidston's opinion that the two races had a common origin is perfectly tenable, but the common source probably lay very far back. The present evidence indicates that the Spermatophytes have been an independent phylum from very early times, and were not derived from Ferns or any of the higher Vascular Cryptogams, but more probably from some long-extinct stock, perhaps comparable to the Psilophytales.

The Pteridosperms, paradoxical as it may sound, are, in fact, too much like Ferns to be descended from them. So close a resemblance in habit (sufficient to deceive almost all botanists from Sir Joseph Hooker downwards) if it indicated affinity at all, must imply a near affinity, which is at once negated by the vast differences in essential characters, *e.g.* seed-reproduction as opposed to homosporous. The most probable interpretation of the facts seems to be, not that the Seed-plants are descended from Ferns, but that the Spermatophytes once passed through a fern-like phase, running parallel with the true Cryptogamic Ferns; they may have sprung, with them, from some quite early race of land-plants. We have no reason to believe that the Seed-plant phylum was ever any more fern-like than the Pteridosperms themselves.

The idea that the Seed-plants were derived from the

Ferns having been abandoned, it may be asked why the former are still included in our scheme under Pteropsida? The justification may be found in the parallelism which undoubtedly exists between the Pteridosperms and the Ferns. Wherever any analogy can be traced between the Pteridosperms and the Cryptogams, whether in anatomy or external morphology, it is with the Ferns alone that comparison is possible. This fact retains its importance, though all belief in any actual filiation of the two classes may be given up.

The more detailed relationships of the families referred to Pteridosperms have already been considered in Chapter III. We have hitherto tacitly assumed that the Pteridosperms represent the earliest type of Seed-plants. It must be pointed out, however, first, that the conception of Pteridosperms is a very vague one; the group no doubt included very heterogeneous members. And secondly, we cannot be sure that all Seed-plants passed through the Pteridosperm phase; there may have been other parallel lines.

Some recent work no doubt tends to link up the two great Palaeozoic groups, Cordaitales and Pteridosperms. *Mesoxylon*, for example, is essentially a *Cordaite* with centripetal wood in the stem, a character suggesting a possible affinity with the type of *Lyginopteris* or *Calamopityx*. In fact, among the Calamopityeae, Zalesky's genus or sub-genus *Eristophyton* seems to approach the Cordaitales.

The most important point of agreement between the two groups is, however, in the seeds, for no constant distinction has been observed between the seeds of Pteridosperms and those of Cordaitales. This community of seed-structure would seem to indicate a close affinity.

The Cordaitales themselves may prove to be a somewhat heterogeneous assemblage. As regards the family Cordaiteae, we have no evidence that they existed in Devonian times, nor do we know much about them in

the Lower Carboniferous—they are essentially an Upper Carboniferous and Permian group. The Poroxyleae, so far as is known, are only of Permo-carboniferous age. On the other hand, the Pityeae are as old as any known Pteridosperms; Zalessky's genus *Callixylon*, an evident ally of *Pitys*, is an Upper Devonian fossil.

It is evident from Dr. Gordon's work, though not yet published in full, that the Pityeae formed a very distinct family as shown by the characteristic foliage and various anatomical peculiarities (see p. 256). They are very different from the other Cordaitales, and show no distinct approach to the Pteridosperms either. It is possible that they may represent a separate line, of relatively early origin. But as we know nothing of their fructification we cannot come to any definite conclusion. We have found it simpler to treat the early Seed-plants provisionally as a single main phylum, though realising that here also diverse parallel lines may be represented¹ (see also below, p. 420).

Prof. F. W. Oliver's interesting discovery of a sporangium (*Tracheotheca*), similar to that of certain Botryopterideae, containing tracheides in the inner layers of its wall,² suggests a certain analogy with seed-structure, and may prove to be a valuable indication. At present, however, the case is too isolated for any phylogenetic significance to be attached to it.

In later Palaeozoic times, the Cycadoxyleae appear (p. 229). Their stems have taken an aberrant line of development, through the suppression of primary wood and the elaboration of anomalous secondary growth, and thus present some analogies with the more modified of

¹ For the latter view see Chamberlain, "The Living Cycads and the Phylogeny of Seed Plants," *American Journal of Botany*, vol. vii. 1920; Sahni, "On the Structure and Affinities of *Acropyle Pancheri*," *Phil. Trans. Royal Soc. Series B*, vol. 210, 1920; Benson, "The Grouping of Vascular Plants," *New Phytologist*, vol. xx. 1921.

² F. W. Oliver, "On a Vascular Sporangium from the Stephanian of Grand Croix," *New Phytologist*, vol. i. 1902, p. 60.

the recent Cycadaceous stems. They may well have been Cycadophyta, though probably not closely allied to the known Mesozoic or recent types.

The relation of the Pteridosperms to the Cycadophyta is clear, and indeed, as we have seen, it is sometimes difficult to draw the line between the two classes. For the present, it is convenient to keep the Pteridosperms distinct, on account of their relatively primitive character, but there is every reason to hope that further discoveries will effectually link them on to the typically Gymnospermous Cycadophyta. The anatomical resemblances, which led to the recognition of the "Cycadofilices," prepared us for the discovery of the seeds, which are sufficient in themselves to demonstrate a near affinity between certain of the Pteridosperms and the Cycads. Curiously enough, the relation is closest with the seeds of the recent Cycadaceae, a group of which the geological history is still obscure. Those of the Mesozoic Bennettitales are not so readily comparable, and evidently represent a more advanced stage of evolution, their seeds having been modified and in some respects simplified in correlation with the development of the complex fruit.

As regards the microsporangiate organs of the Pteridosperms, our present somewhat scanty information indicates that they were of the nature of synangia (p. 77); they thus find a remarkable analogy in the compound pollen-sacs of the Mesozoic Bennettitales (p. 345). The sporophylls, so little differentiated from the vegetative foliage, may be compared with the stamens of Bennettitaceae on the one hand, or with the foliaceous carpels of *Cycas* on the other.

The question whether the Lyginopterideae or the Medulloseae were the nearer to the main line of Cycadophytic evolution may be a sterile one, for there were many other races of Pteridosperms, among which the true ancestry may lie concealed. A few points of comparison may, however, be noted. So far as the anatomy of the stem

is concerned, *Lyginopteris* shows analogies with the Cycads, for the general organisation is of a similar character, and the mesarch structure of the bundles is still retained in the peduncles of the cones of some recent Cycads as well as in the leaves (p. 27). The habit and anatomy of the *Lyginopteris* foliage is, however, unlike anything known either in Mesozoic or recent Cycadophyta.¹ It has been suggested that *Lagenostoma*, the seed of *Lyginopteris*, may have given rise to the seed of Cycadaceae by the cupule becoming adherent to the integument, and thus constituting the supposed outer integument of the Cycadean ovule.² This view, however, assumes that the integument of the seed in recent Cycads is double, an interpretation which is open to much doubt.

Seeds of the *Trigonocarpus* type (p. 204), referable to Medulloseae, appear to have much in common with those of the Cycadaceae, as shown by the drupe-like differentiation of the testa, the double vascular system, and the form of the pollen-chamber. The chief difference lies in the free nucellus of the Trigonocarpeae, which contains the inner vascular system, whereas in the Cycadaceae the nucellus is adherent to the integument, and the inner vascular system appears usually to belong to the latter, though in *Bowenia* it is described as nucellar. In spite of these differences, I am inclined to regard the *Trigonocarpus* type as the nearest approach among Pteridosperms, so far as we know at present, to the seed of the Cycadaceae.

¹ It is conceivable that a phyllodineous reduction of a leaf of the *Sphenopteris* type might lead to a structure not unlike that of the leaf in the genus *Cycas*, with uninervate pinnae. The very curious Annam species, *C. Micholitzii*, Dyer, with quadrifid pinnae, is of interest from this point of view. See *Gardener's Chronicle*, August 19, 1905.

² M. C. Stopes, "Beiträge z. Kenntnis der Fortpflanzungsorgane der Cycadeen," *Flora*, Bd. xciii. 1904; "On the Double Nature of the Cycadean Integument," *Ann. of Bot.* vol. xix. 1905. Cf. Salisbury, "On the Structure and Relationships of *Trigonocarpus shorensis*," *Ann. of Bot.* vol. xxviii. 1914, p. 72.

Anatomically, the Medullosean stem differs from that of recent or Mesozoic Cycadophyta in being polystelic (except in the peculiar protostelic *Sutcliffia*). Certain local peculiarities in the vascular system of various Cycads, due to anomalous distribution of the cambium, have been interpreted as relics of a polystelic structure, but these exceptional irregularities do not appear to bear more than a superficial resemblance to the primary polystely of the Medulloseae.¹ The theory of a possible derivation of the Cycadales from a monostelic line of Medulloseae represented by *Sutcliffia* has already been discussed (p. 219).

It is a significant fact that the structure of the petiole and the organisation of the leaves generally are very similar in Medulloseae and Cycadaceae, and the resemblance extends to the Bennettiteae of the Mesozoic. On the whole of the evidence available it appears likely that some at least of the Cycadophyta may have been derived from plants resembling the Medulloseae (Neuropterideae) in certain characters, though probably with monostelic rather than polystelic structure of the stem.

Leaving the Cycadophyta for the moment, we may now further consider the relation of the Pteridosperms to the Cordaitales, the characteristic Gymnosperms of the Palaeozoic. In some respects two groups of plants could scarcely appear more different than the Fern-like Spermatophyta and the family Cordaiteae. In habit there is no resemblance, the Cordaitean trees having externally much more in common with Araucarian Conifers than with any of the known Pteridosperms (pp. 267, 269). The specialised cones or catkins of the Cordaiteae, grouped

¹ Some of the most striking cases of so-called "polystely" among recent Cycads occur in the *root*, an organ which in the Medulloseae was monostelic. For the polystelic interpretation of Cycadean structure see Worsdell, "Structure and Origin of the Cycadaceae," *Ann. of Bot.* vol. xx. 1906, p. 129; Matte, *Récherches sur l'appareil libéro-ligneux des Cycadacées*, 1903.

in inflorescences, are wholly remote from the compound, scarcely differentiated sporophylls, springing from the main stem, which bore the seeds and pollen-sacs in the Pteridosperms. The Cordaiteae are altogether on a far higher level of organisation, and deserve the place among true Gymnosperms which has always been assigned to them.

There are, however, marked indications of affinity between Pteridosperms and Cordaitales, great as the differences between them appear. The strongest mark of affinity, as already pointed out, is in the seeds, which are essentially of the same type in the two groups. Of seeds already known in detail, the closest agreement is between the *Trigonocarpus* group and the Cordaiteae (p. 204); they have in common the double vascular system, the drupe-like testa, the form of the pollen-chamber, and probably the free nucellus. On the other hand, they differ in the fact that the Trigonocarpeae are radiospermic, the Cordaiteae platyspermic, but this distinction has no general validity, for we have good evidence that bilateral as well as radial seeds occurred among the Pteridosperms (pp. 220, 222).

Rhabdocarpus, attributed to *Poroxylon* by Grand'Eury, only differs in small details from the seeds of the family Cordaiteae (p. 252). We know nothing as yet of the seeds of the somewhat isolated group Pityeae, the third family making up our class Cordaitales.

As regards the anatomy, there is a very complete series leading from the stem of the Lyginopterideae to that of the typical Cordaiteae, as described by Renault. In *Calamopityx* (*Eristophyton*) we find the first signs of the dying out of the centripetal wood in the lower part of the leaf-trace bundle (pp. 124, 127). In *Poroxylon* the same condition recurs, with a general structure much like that of *Cordaites* itself (p. 248). In the Lower Coal-measures the stems of *Mesoxylon*, otherwise indistinguishable from those of *Cordaites*, have well-marked centripetal wood in the stem (p. 275). The Pityeae have, however, a quite

peculiar arrangement of the primary xylem, suggesting a distinct line of descent, supported, as we have seen, by the characteristic foliage, discovered by Dr. Gordon. It is at least an interesting point that the older Cordaitalean stems generally show some trace of the centripetal wood, while it seems to have disappeared in the late Carboniferous or Permian species of *Cordaitea* which Renault investigated. Concurrently with the gradual extinction of the old Cryptogamic wood, we find on the whole a tendency to greater density of the secondary wood, with a diminution in the width of the medullary rays. The double leaf-trace is a common, though not a constant, character at all stages, the division of the trace extending, on the whole, lower down into the stem in the later forms. Other details, such as the structure of the outer cortex, are also common to many members of the series, from the Lower Carboniferous Calamopityeae to the Permian Cordaiteae. Without for a moment supposing that we have here the actual course of evolution before us, the series seems to afford some support to the theory that the Cordaitales (apart from the Pityeae) sprang from a Pteridospermous stock, while the leaf-structure supports this conclusion, the mesarch or exarch foliar bundles of Poroxyleae and Cordaiteae being a distinctly Pteridospermous character. On the evidence of the seed-structure and the anatomy together, the affinity of certain Cordaitales with the Pteridosperms seems to be well supported, though in point of time the connection must lie very far back. The question of the Pityeae must be left open.

The various Cycad-like characters which have long been remarked in both vegetative and reproductive organs of the Cordaiteae are doubtless not to be explained by any direct relation to the Cycads, but may suggest a common descent from an early Pteridospermous stock.

The possible Pteridospermous affinities of the Cor-

daiteales have an important bearing on the question of the systematic position of the Coniferae. It has generally been recognised that the family Cordaiteae is related to the Coniferae, and if this be so, it follows that the latter may also have been ultimately of Pteridospermous descent, and thus find a place in the great phylum of the Pteropsida.

Some authors, however, have endeavoured to derive the Conifers from the Lycopodiales,¹ while others have limited this theory to a portion only of the Coniferae,² implying that the order is an artificial assemblage, made up of at least two unrelated groups.

Prof. Seward regarded the Araucarieae as probably of Lycopodineous origin, while he left the question open for the rest of the Coniferae.³ Recently he has expressed the opinion that the Conifers are probably monophyletic. Some brief discussion seems necessary here, as the issue involved is that of the single or multiple origin of the existing Spermatophyta. The position of the Araucarieae will be primarily considered, since it is this group especially which has been in dispute.

The Araucarieae present a close agreement with the Cordaiteae in the structure of the stem, and especially in that of the wood, which, as universally admitted, is often indistinguishable in the two families. The essential feature is that the mass of the wood, apart from the medullary rays, is composed of tracheides with multi-seriate bordered pits on their radial walls. This is the

¹ E.g. D. H. Campbell, *Lectures on the Evolution of Plants*, New York, 1899, pp. 166-167.

² E.g. H. Potonié, *Lehrbuch der Pflanzenpaläontologie*, Berlin, 1899, p. 320. Also the new edition by Gothan, 1921, p. 485.

³ A. C. Seward and S. O. Ford, "The Araucarieae, Recent and Extinct," *Phil. Trans. Royal Soc. B*, vol. 198, 1906, pp. 305-411. For Seward's later views see his *Fossil Plants*, vol. iv. 1919, p. 166. See also R. Boyd Thomson, "On the Comparative Anatomy and Affinities of the Araucarineae," *Phil. Trans. Royal Soc. B*, vol. 204, 1913, and L. Burlingame, "The Origin and Relationships of the Araucarians," *Bot. Gazette*, vol. lx. 1915.

characteristic type of wood throughout the Cordaitales and Pteridosperms, while it is practically unknown among Lycopods,¹ in which the tracheides are very constantly scalariform. The absence of centripetal wood in the Araucarian stem presents no difficulty on the hypothesis of Cordaitean affinity, for its gradual disappearance in certain Pteridosperms and in the older Cordaitales can be traced, until it is lost in the stems of the typical Cordaiteae. No such links with the stem-structure of Lycopods are known.

The roots in Araucarieae (and Conifers generally) are essentially of the same type as in Cordaitales, and show none of the peculiarities of Lycopod roots.

The leaves of Araucarieae, with their numerous parallel bundles, agree generally, though not in detail, with those of Cordaiteae. That the multinervate character is primitive is indicated by the fact that the cotyledons likewise contain several bundles. Lycopods as a rule have only one foliar bundle, which, in the case of *Sigillariopsis*, divides into two. If the Araucarieae are relatively primitive Conifers, a point on which I am disposed to agree with Prof. Seward, it appears that the more complex type of leaf-structure is the original one for the Order. While the general anatomy of the leaf is thus entirely favourable to Cordaitean affinities, the histology lends no decided support to either view of the affinities. The vascular bundles have no typical centripetal wood, but are accompanied by transfusion-tissue, which we may either regard, with Mr. Worsdell and M. Bernard, as representing the centripetal xylem of Cordaiteae,² or may compare with the well-developed transfusion-tissue occurring in fossil Lycopods. On any

¹ The only case I know of is in Renault's *Sigillariopsis Decaisnei*, where some of the tracheides are pitted, though they do not appear to agree at all closely with those of the Araucarieae.

² It will be remembered that, according to Dr. Stopes's observations, transfusion-tissue, as well as centripetal xylem, occurs in the Cordaitean leaf (p. 290).

view, the centripetal part of the xylem is a tissue which becomes modified or lost in the higher plants.¹

Passing on to the organs of reproduction, the male cones of *Araucarieae* show some points in common with those of *Cordaiteae*. As we have seen, the stamens of the latter group have been well compared with those of *Ginkgo*. The stamens of *Araucarieae*, with their distally attached pollen-sacs, are of the same type as in *Ginkgo*, but the large number of the sacs brings them nearer to the *Cordaitean* stamen; on the other hand, they differ absolutely from the sporophylls of the *Lycopods*, in which the constant relation of one sporangium to one sporophyll is a character diagnostic of the class.² The numerous nuclei in the pollen-tube of the *Araucarieae* present a manifest analogy, as Prof. Seward recognises, with the multicellular pollen-grains of *Cordaiteae* and *Pteridosperms*. At present we know nothing of the fertilisation of the "seed-bearing" *Lycopods*, so on this side the material for an equally close comparison is wanting.

The female cones of the *Araucarieae* alone appear to afford any support to the *Lycopod* theory. The single ovule on the upper surface of the cone-scale offers an evident analogy with the sporangium and sporophyll of a *Lycopod*, though if the Cretaceous *Protodammara*, with three ovules on each scale, is rightly referred to *Araucarieae* (p. 380), the value of the analogy becomes very doubtful. In any case the vascular system of the *Araucarian* cone-scale is totally different from anything in the sporophylls of *Lycopods*. The comparison between

¹ The structure of *Araucarian* seedlings obviously cannot be used in the comparison with a fossil group. Recent work, however, shows that the anatomy of the seedling in *Araucarieae* conforms to the same type as that of the *Cycadaceae* and *Ginkgo*, while other *Coniferae* show a modification of the type in the direction of reduction.

² The comparison of the *Araucarian* stamen with the sporangiophore of *Cheirostrobis*, suggested by Prof. Seward, is interesting, but by no means supports a relation to the *Lycopods*, with which *Cheirostrobis* can only have the most remote affinity.

Araucaria, in particular, and *Lepidocarpon*, on which Prof. Seward lays stress, appears to amount to no more than a distant analogy, for the part which envelops the ovule in *Araucaria* is not, as in *Lepidocarpon*, the integument itself, but an extra covering enclosing an already integumented megasporangium.¹

Until the nature of the so-called ligule, and, generally, the relation of the female cones of Araucarieae to those of other Coniferae, are cleared up (which is far from being the case at present), it is useless to compare these strobili with fossil fructifications. It appears probable, however, that the comparison of the cone-scales with Lycopod sporophylls, though seductive, may be fallacious, the great complexity of the Araucarian cone-scale suggesting that the resemblance is limited to external characters. In particular, there seems to be little likeness, except in name, between the ligule of the higher Lycopods and the structure called the "ligule" in the Araucarians.

The absence of a pollen-chamber in the Coniferous ovule is no doubt correlated with the abandonment of fertilisation by spermatozoids.

Without extending the discussion further, it may, I think, be concluded that the Araucarieae have many points in common with the Cordaitales, of sufficient weight to establish a real affinity, while the resemblances to the Lycopodineae are of a more doubtful and superficial nature, and appear to be completely outweighed by the great differences which separate these two groups.

Since the Araucarieae have been chosen as the family most favourable to the Lycopod theory of Coniferous descent, it does not seem necessary to discuss the question for the other families. The idea that the Coniferae include two wholly diverse groups, belonging to distinct phyla, appears to me quite untenable—either all are Lycopsida or all Pteropsida. The separatist view, which

¹ See Figs. 25 and 26, p. 362 of Seward and Ford's *Araucarieae*.

is probably no longer maintained, arose from paying attention too exclusively to particular organs rather than to the whole sum of characters.

Taking all the characters into account, there thus appears to be a decisive balance of evidence in favour of deriving the whole of the Coniferae from the Cordaitales, in a wide sense, without tracing them through the particular family Cordaiteae (of which, after all, our knowledge is still very narrow). The Conifers thus fall within the great division Pteropsida, though in their case the analogies with Ferns have disappeared. This view involves the conclusion that the microphyllous habit, which characterises so many of the Coniferae, is the result of reduction in the leaf, correlated with the increasing ramification of the stem, and also expressing a more perfect adaptation to the conditions of life on dry land.¹

The relations of the Ginkgoales to the Cycads and Cordaiteae are universally admitted, and need not be further discussed here (pp. 311, 384).

The characteristic Mesozoic Cycadophyta, the Bennettitales, were fully considered in the last chapter. Although the fossil Angiosperms do not fall within the scope of these "Studies," a few words may be added on the relation of the great modern sub-kingdom to the scarcely less dominant Cycadophyta of the Secondary Period.

The general arrangement of the organs in the Bennettitalean fructification, as shown by Dr. Wieland's classical

¹ I have purposely refrained from discussing the views of Prof. E. C. Jeffrey and his school, according to whom the Abietineae are the most primitive Conifers and the Araucarieae are derived from them. Such a discussion would demand a much fuller consideration of the Coniferae than is possible here. For a summary of Prof. Jeffrey's theory, see his *Anatomy of Woody Plants*, 1917, chap. xxiv. For criticisms, see the papers on Araucarieae above cited; also Gothan, *Potonié's Lehrbuch*, 1921, p. 342; and Seward, *Fossil Plants*, vol. iv. 1919.

investigations, is essentially the same as in a typical Angiospermous flower, with a central pistil, a surrounding whorl of stamens, and an enveloping perianth (see pp. 343, 375). The whole organisation, as Dr. Wieland at once recognised, is best compared with that of the flower in Magnoliaceae, such as the Tulip-tree (*Liriodendron*), while the resemblance extends to other orders of polypetalous Dicotyledons, *e.g.* Ranunculaceae and Nymphaeaceae. The occurrence, in some cases, of unisexual flowers does not affect the comparison. These groups, especially the Magnoliaceae, have been widely accepted as relatively primitive, and there is evidence for their occurrence in Cretaceous rocks.

As we have seen, the gynaecium of Bennettitales shows some approach to the condition of a closed Angiospermous ovary, while the seed of *Bennettites* was practically exalbuminous, the large Dicotyledonous embryo filling the embryo-sac—a feature otherwise met with only among the Angiosperms.

Taking the whole of the characters into consideration, the evidence for some affinity between the Mesozoic Cycadophyta and the Angiosperms appears strong. It cannot, of course, be supposed that the Bennettitales were on the direct line of Angiospermous descent, for there are manifest points of difference, notably (apart from the anatomy) in the complexity of the stamens (though this was by no means constant) and in the organisation of the ovary-wall or pericarp, which was not formed by the carpels themselves, but by the associated sterile scales. The connection was probably nearer with the older Williamsonian tribe than with the specialised Bennettiteae themselves. Dr. Wieland points out that in *Wielandiella* and *Williamsoniella* the branching was but little simpler than in some Magnolias.¹ There is much difference of opinion as to the nearness of the relation between Bennettitales and the higher

¹ *Fossil Cycads*, vol. ii. pp. 54 and 219.

Flowering Plants; some would reduce it to a mere analogy; but the points of agreement are so striking that we may fairly conjecture that a real relation may exist, and that the ancestry of the Angiosperms, hitherto the most obscure subject in the phylogeny of plants, may perhaps be sought somewhere among the great plexus of Cycadophytes, which overspread the world during the Mesozoic Period.¹

This conclusion opens up the question of the relation of Monocotyledons to Dicotyledons. If the Angiosperms are related to Cycadophyta, it would appear to follow that the Dicotyledons were first evolved, for their structure has clearly much more in common with the Cycad type than that of the Monocotyledons. The latter would thus be regarded as a branch line of descent, diverging, no doubt at a very early stage, from the main Dicotyledonous stock. This view has been maintained, on other grounds, by various modern botanists. So far, however, as the palaeontological record shows, the two classes are of almost equal antiquity, both being recorded for the first time in Lower Cretaceous rocks.² By the Upper Cretaceous age the Angiosperms had already seized the dominant position which they now hold; the Monocotyledons were always subordinate in numbers to the other class, but the occurrence of typical Palm-wood in Cretaceous rocks is a striking proof of the early evolution of one of the most characteristic Monocotyledonous families.³

The relation of the Bennettitales to the Pteridosperms

¹ See Arber and Parkin, "The Origin of Angiosperms," *Journal Linn. Soc. (Bot.)*, vol. xxxviii. 1907.

² The discovery of several distinct types of highly organised Dicotyledonous stems in the Lower Greensand, shows that the history of this class must run enormously further back than it has yet been traced. See Dr. Marie C. Stopes, *Catalogue of the Cretaceous Flora*, vol. ii. 1915, pp. 258-294.

³ The very remarkable Middle Jurassic fruits (*Caytonia* and *Gristhorpia*) discovered by Mr. Hamshaw Thomas, but not yet fully described may throw a new light on the question of Angiospermous evolution.

has been sufficiently emphasised in preceding pages. We are thus led to the conclusion that the whole of the Angiospermeae, the dominant sub-kingdom of Flowering Plants, if akin, as is suggested, to the Cycadophyta, belonged ultimately to a phylum which, from its analogy with the Ferns, is included in Pteropsida. We may add that the Gymnosperms, as a whole, may probably be referred to the same stock, for evidence has been adduced that the small group of the Gnetales (the only outstanding Gymnospermous family) may have been derived, by reduction of the floral organs, from forms allied to the Bennettitales.¹

It thus appears, if the views here taken are justified, that the whole of the Spermatophyta, whether Angiospermous or Gymnospermous, may have been ultimately derived through primitive Seed-plants of the nature of Pteridosperms, from one ancient stock, which may likewise have been the ultimate source of the Ferns. With this far-reaching hypothesis we may conclude our consideration of the phylogenetic results of our studies.

In bringing these "Studies" to a close, it is well to recall the necessary limitations of all attempts to unravel the past history of organisms. Our ideas of the course of descent must of necessity be diagrammatic; the process, as it actually went on, during ages of inconceivable duration, was doubtless infinitely too complex for the mind to grasp, even were the whole evidence lying open before us. We see an illustration, on a small scale, of the complexity of the problem, in the case of domesticated forms, evolved under the influence of man. Though we know that our cultivated plants, for instance, have been developed from wild species within the human period, and often within quite recent years, yet nothing is more difficult than to trace, in any given

¹ Arber and Parkin, "Relationship of the Angiosperms to the Gnetales," *Annals of Botany*. vol. xxii. 1908.

instance, the true history of a field-crop or a garden plant, or even, in many cases, to fix its origin with certainty. In the history of natural groups, where the geological record takes the place of the cultivator's notes, the problem increases so immeasurably in difficulty that a full solution becomes impossible.

But although, in endeavouring to form an idea of the course of evolution of any part of the Vegetable Kingdom, we can only hope, at the best, to construct a scheme, representing in a much simplified form the real succession of events, we must take care not to be misled by our own constructions. We must remember that, at all periods, competition among living things was as keen as now, and that in every age all the available places must soon have been filled. Hence, even in the earliest times of which the palaeontologist takes cognisance, there must always have been specialised forms, and even what we call "synthetic" types were themselves specialised to suit some particular set of conditions. Thus, at every step in the investigation of the fossil evidence, the same caution in distinguishing between the newer and the older characters is demanded as when we are dealing with recent organisms.

The present difficult position of the Theory of Descent, now that the Darwinian period, with its confident outlook, has passed by, imposes greater caution than ever on our speculations. In our complete ignorance, now realised, of the methods of Evolution, we cannot hope for very definite success in tracing its course. A more tentative and diffident tone seems to be demanded in discussing phylogenetic problems, and may be found, it is hoped, in the present issue of this book.

Yet, in spite of all these difficulties, and others, more obvious, which will at once occur to the mind, there can be no question that the study of the actual records of the past is of inestimable value in attacking a problem which is in its essence an historical one.

In these "Studies" the fossil record has been considered almost wholly from a morphological and evolutionary point of view. There is room, even with the material already available, for important work on other lines. The subject of the biology and ecology of fossil plants, as illustrated especially by their physiological anatomy when suitably preserved, offers a wide and promising field of research. Such biological studies would be of the greatest intrinsic interest, and may also throw a new and welcome light on the problems of Evolution.

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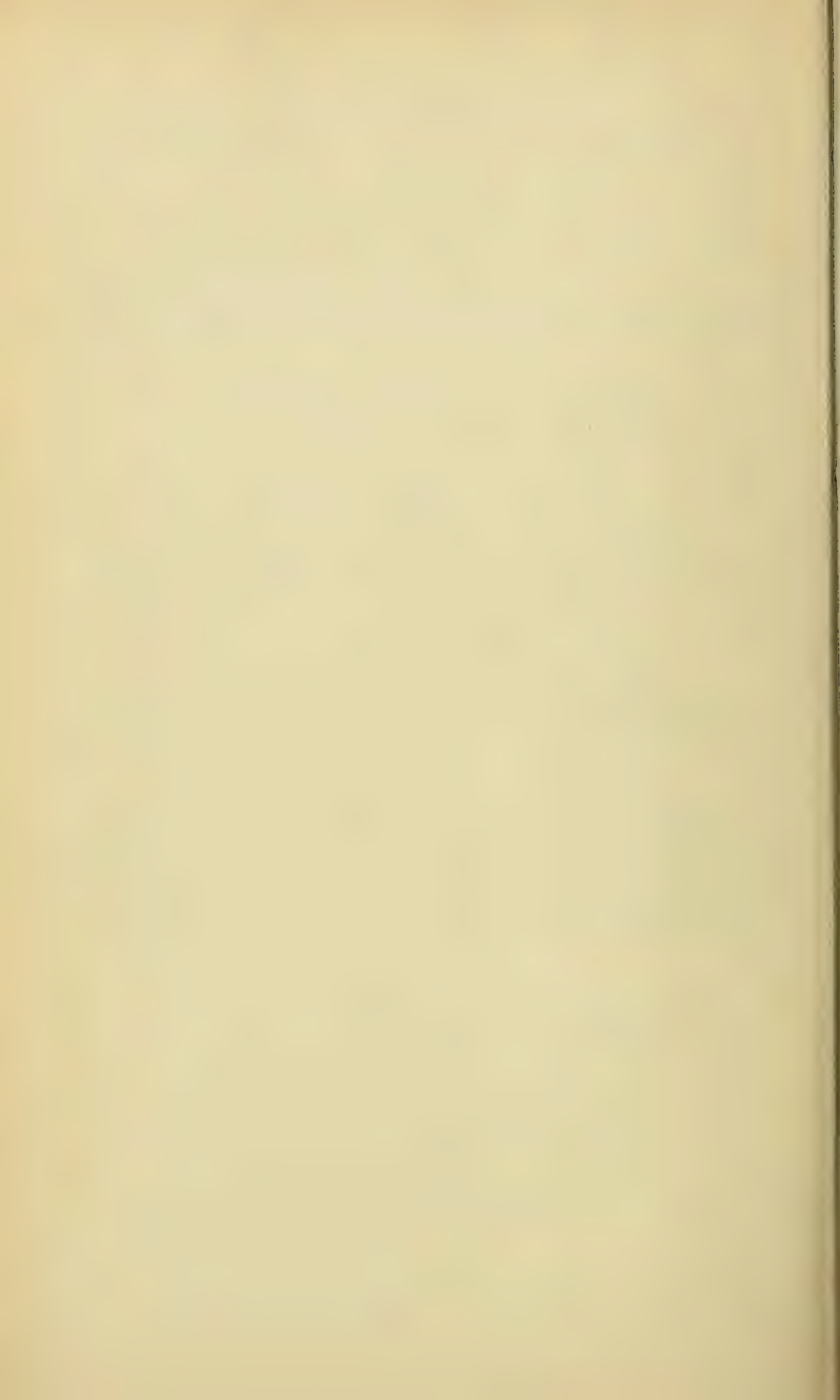
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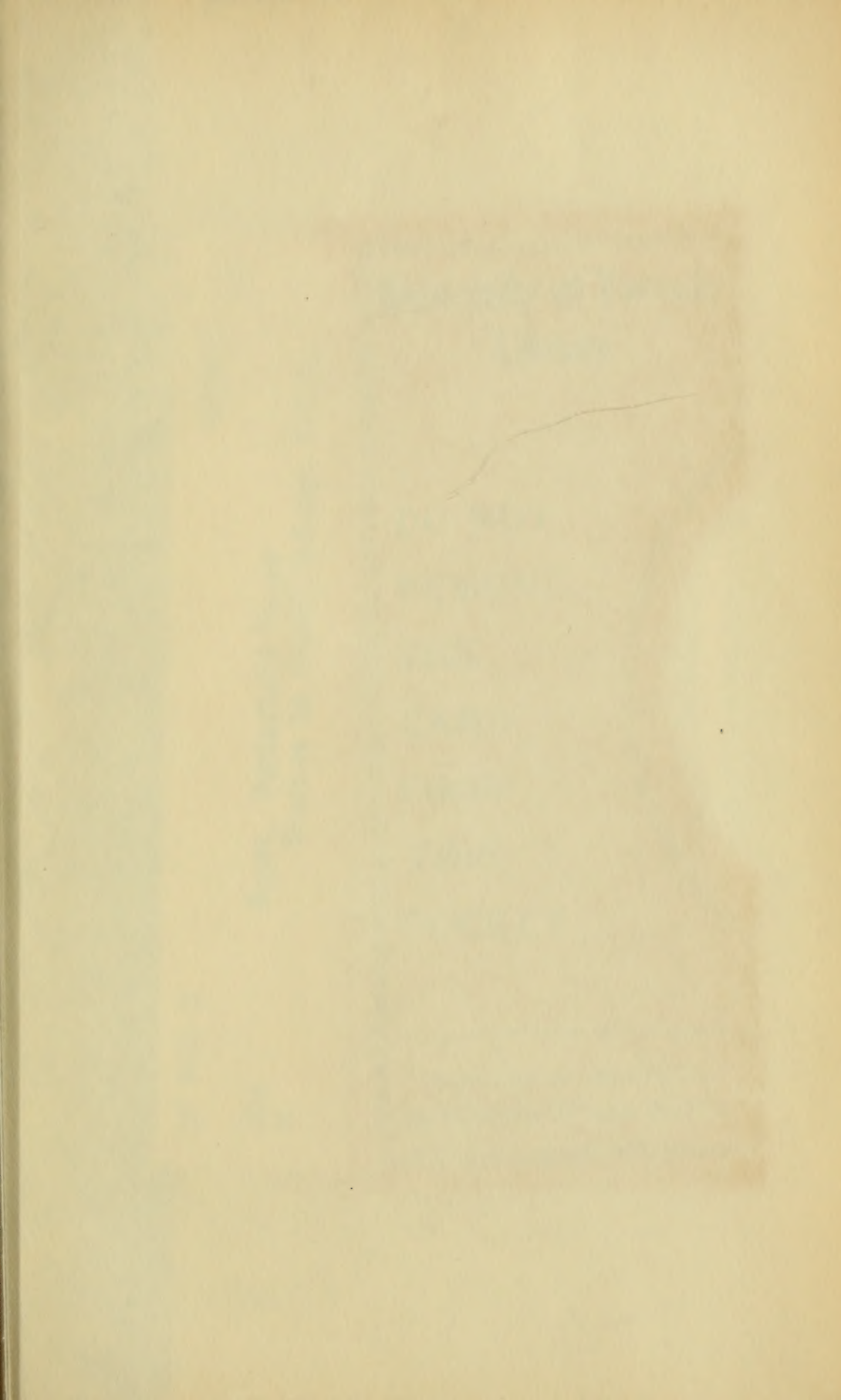
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